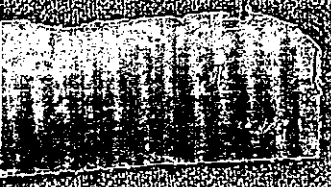

ESTIMATING POPULATION CHANGE AND DISPERSAL ACTIVITY OF SPIDERS IN AN AGRICULTURAL LANDSCAPE

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Ph.D.

2009

ESTIMATING POPULATION CHANGE AND DISPERSAL ACTIVITY OF SPIDERS IN AN AGRICULTURAL LANDSCAPE

By

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A thesis submitted to the University of Plymouth

in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

School of Biological Sciences

Faculty of Science

November 2009

ESTIMATING POPULATION CHANGE AND DISPERSAL ACTIVITY OF SPIDERS IN AN AGRICULTRAL LANDSCAPE

CHRISTOPHER WOOLLEY

The principal aims of this work were to investigate dispersal activity of spiders commonly found in agricultural crops, and to study the influence of both crop type and farm operations on spider assemblages and populations. Work was also conducted to develop and test an improved trapping method for sampling aerially dispersing (ballooning) spiders. Objectives were to determine whether common farmland species exhibited species-specific differences in dispersal activity. Behavioural data from wind chamber studies were also related to field data to establish if seasonality in dispersal was related to seasonal changes in dispersal motivation or variation in ground population densities. Ground population data were used to determine if field-scale differences in spider assemblage were related to crop type, and if crop-specific management was associated with variable impacts on spider populations.

The improved trapping method ('stick and bottle' trap) was observed to increase catch sizes significantly ($F_{(1,18)} = 30.11$, $P < .0001$) compared to climbing-sticks with trapping adhesive. Total catch size over an eleven day period was 564 spiders. The use of an 'interception net' increased catch sizes threefold. Average loss of spiders from the traps was $9.1\% \pm 7.7\%$ for daylight hours between 09:00 and 17:00.

The common linyphiid spiders *Erigone atra*, *Oedothorax fuscus* and *Tenuiphantes tenuis* were observed to display different patterns of dispersal over time. Patterns were similar for closely related species. Under wind chamber conditions, ballooning related activity in *E atra* comprised almost one third of total activity time yet was vitually absent in *O. fuscus*. *Erigone atra* was observed to balloon more frequently than *O. fuscus* in the field - it is suggested that factors influencing the tendency to balloon are different for these species. Ground populations related positively to ballooning activity for *Oedothorax* spp. females and *E dentipalpis* males. For other species the high efficiency of the trapping method may have reduced applicability to local ground populations Seasonal differences in ballooning motivation observed in *E atra* females in the wind chamber were likely related to differences in seasonal temperature affecting activity and not ballooning motivation

Variation in spider assemblage composition was observed for fields under different management and crop production. Correspondence analysis suggested vegetation structure may influence the abundance of some species Set-aside was observed to have a higher proportion of non-linyphiid species than other fields *Oedothorax fuscus* was dominant in almost all crops which could relate to its affinity for grass leys which predominate in the landscape.

Harvesting in cereals and grass were seen to negatively impact spider populations with declines of 96% and 83% observed respectively within nine days of harvesting Post harvest emigration was thought to contribute to these reductions Harvesting in maize however had a negligible impact on spider populations with relative high densities of adults overwintering in maize stubble

Index of Figures

Index of Tables

Index of Appendices

Acknowledgements

This work was funded through BBSRC grants D14032, D20476 and D14036

I wish to express my thanks to

My supervisors Dr George Thomas and Prof Rod Blackshaw

My family; Mum, Ian, Dad and my brother Jason for his assistance with 'number crunching'.

To the staff of University of Plymouth and the former Seale-Hayne Faculty, particularly all the Ag. Lab Staff, Peter Russell, Carolyn Streets, Patrick Bugg, Keith Jarvis, Ashley Noyce, Rick and Katie for their assistance over the years and Mr Aylıffe for allowing me to carry out sampling in his fields.

Prof Linton Winder for his very useful comments on my drafts and Peter Smithers for his assistance with checking identifications

Thanks to all my friends who helped keep my spirits up and Sally for her support throughout, Ken and Julia who looked after me during my write-up and Sarah, Toad and especially Helen for her crisis management skills when they were most needed!

I would also like to thank my wife Caroline for her love and support.

AUTHORS DECLARATION

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other university award without prior agreement of the Graduate Committee.

This project was funded through BBSRC grants D14032, D20476 and D14036 and was part of a collaborative project with the University of Cambridge and University of East Anglia. Related work carried out at each instituation was conducted independently and all work detailed in this thesis was performed soley by the author.

Relevant scientific seminars and conferences were attended at which work was presented; external institutions were visited for consultation purposes.

Publications:

Woolley C, Thomas CFG, Hutchings L, Goodacre S, Hewitt GM, Brooks SP (2007) A novel trap to capture ballooning spiders. *The Journal of Arachnology* **35**, 307-312.

Thomas CFG, Blackshaw RP, Hutchings L, Woolley C, Goodacre S, Hewitt GM, Ibrahim K, Brooks SP, Harrington R (2003) Modelling life-history / dispersal-strategy interactions to predict and manage linyphiid spider diversity in agricultural landscapes. In 'Proceedings of the 1st Landscape management for Functional Biodiversity Study Group'. Bologna (Italy). (Eds W A.H., H-MP Rossing and G Burgio) pp. 167-172. (IOBC wprs Bulletin).

Presentations and conferences attended:

The Royal Entomological Society 'International Symposium on Insect Conservation Biology', 12-14 September 2005, University of Sussex, UK

Dartmoor Diversity Group,

October 2003, University of Plymouth, UK

IOBC / WPRS 'Landscape Management for Functional Bidiversity',

11-14 May 2003, Bologna, Italy

Postgraduate Forum

April 2003, University of Plymouth, UK

British Ecological Society Winter Meeting,

18-20 December 2002, University of York, UK

Devon Invertebrate Forum

March 2002, Devon Wildlife Trust, Exeter, UK

Word count of main body of thesis: 53034

Signed ....

5/11/09 *Date*

Chapter 1. Introduction

1.1 Spiders (Araneae, Arachnida)

1.1.1 A general description

Spiders (order Araneae) and their relatives such as the mites (order Acari) and scorpions (order Scorpiones) belong to the class Arachnida which, as jointed-limbed invertebrates, are members of the phylum Arthropoda together with familiar groups such as the insects (class Insecta), millipedes (class Diplopoda) and the crabs and lobsters (class Malacostraca). Spiders are, with few exceptions, terrestrial animals which unlike insects do not possess wings or antennae. Four pairs of ambulatory limbs are present in addition to an anterior pair of appendages adapted for feeding, reproduction and grooming. Another distinct feature is the body being divided into two major parts, the prosoma, or cephalothorax, and the opisthosoma, or abdomen. The prosoma comprises the fused head (*cephale*) and thoracic sections and is joined to the abdomen by a short, narrow waist called the pedicel. All appendages are attached to the cephalothorax. Dorsally this takes the form of a hard, chitinised shield called the carapace. To the front of the carapace are usually six to eight eyes. The clypeus below is the intervening space dividing the eyes and the carapace's edge, beneath which are attached the mouthparts. On the ventral side is a smaller shield-like plate called the sternum which lies between the coxae (first basal sections) of the legs. In most spiders the only obvious division of the body is between the cephalothorax and abdomen, although an ancestral segmentation of the abdomen is retained in extant species of the suborder Mesothelae. In comparison to the hard cephalothorax, the abdomen is usually soft and 'sac-like' containing the gonads and the major respiratory, circulatory and excretory organs. The

abdomen also carries terminal processes (although positioned medially in the Mesothelae) known as spinnerets, which are concerned with silk production, this being a defining characteristic of all spiders. Spiders are predators and silk may be spun into webs to capture prey or used in the construction of retreats, eggsacs, and in aiding movement and dispersal. All spiders, with the exception of the family Uloboridae and certain primitive Mesothelae, also deliver poison in their bites to subdue and kill their prey. Spiders do not imbibe solid food and therefore their prey, or rather the softer parts, must be reduced to a liquefied state before ingesting This is achieved by the spider regurgitating digestive enzymes directly through the cuticle at the bite or when the prey is being masticated Digestion then occurs partially externally and once ingested continues in the midgut system which runs extensively throughout the spider's body .

1.2 Spiders in the agricultural landscape

1.2.1 Recent changes in agriculture

Agriculture is the world's most extensive industry which in the course of its development has profoundly altered the landscape of many countries (New 2005). In Europe agriculture represents the dominant land use (Robinson and Sutherland 2002).

As on the continent, agriculture in the United Kingdom is well established Historical development has been both gradual, such as the 'Agricultural Revolution' (1620 – 1850) which saw the completion of land enclosure and the introduction of new crops and practices (Grigg 1989), and rapid, as in the recent post WWII 'intensification' (Robinson and Sutherland 2002). Agricultural development in the last 60 years has

brought about significant changes in farming practice. The defining characteristics of the current intensive system are:-

- Consolidation to fewer, larger farms
- Extensive use of mechanisation for most arable operations and subsequent reduction in manual and animal labour with a decline in the need for fodder crops
- Larger fields and reduction in field margins (larger area to boundary ratio)
- Decrease in hedgerows from 0.9×10^6 km in the mid 1950s to 0.4×10^6 km in the early 1990s – DEFRA (Department of Environment, Food and Rural Affairs) statistics
- Increased specialisation into arable or pastoral farming leading to a geographical separation; arable in SE England and pastoral/mixed in the SW England
- Increased use of herbicides allowing continual cereal cropping with no rotation (monocultures)
- Increased use of pesticides
- Increased use of inorganic fertilizers
- Increase in autumn sown cereals and decrease in fields left fallow (in stubble), and reduction in under-sowing
- Increased crop yields

(Robinson 1997; Robinson and Sutherland 2002)

A significant portion of European biodiversity is associated with the agricultural habitat (Robinson and Sutherland 2002) and it is widely recognised that intensification of agriculture has resulted in a decline in many taxa (Donald 1998) The decline in farmland birds (British Trust for Ornithology statistics at http //www.bto org/bbs/index htm) has been particularly well documented owing to high quality monitoring data for this popular group (Donald 1998) Invertebrates have also decreased in abundance. A study on conventionally farmed land in Sussex between 1971 and 1989 (Aebischer 1990) found significant declines in spiders (Araneae), harvestmen, (Opiliones), rove beetles (Staphylinidae), parasitoid hymenoptera (Apocrita, Parasitica) and sawflies (Symphyta) Macro-moths (Lepidoptera) have reduced markedly with declines evident in two thirds of 337 monitored species (Conrad, Warren *et al* 2006). Over a number of decades flower rich hay meadows have become increasingly rare (Wilson 1992) as have historically common arable weeds such as *Agrostemma githago* L (corncockle) and *Ranunculus arvensis* L (corn buttercup)

Implicated in these declines is the increased use of pesticides (Greig-Smith 1990) Modern pesticides are more specific i.e. less toxic to non-target species and less persistent However from the mid 1980s to 2000, although the weight of active chemicals applied decreased, the number and extent of applications increased (Robinson and Sutherland 2002), the environmental impact of which is arguably greater The move to autumn sown crops and the loss of fields in fallow and non-crop habitats such as hedgerows and field margins, have also contributed to declines. These landscape features tend to be disturbed at different times or to a lesser extent than the surrounding managed land and therefore often support higher biodiversities (Samways 1994) and act as refuges for pest controlling invertebrates (Sotherton 1984).

Recent policies have attempted to ameliorate the agricultural environment albeit sometimes indirectly. For instance, reforms to the Common Agricultural Policy to control overproduction in Europe led to the implementation of 'set-aside' that is, land taken out of production for which farmers are compensated financially. Rotation and non-rotational set-aside has increased stubble and pasture-like habitat, however, the percentage of land required to be designated set-aside has fallen from 15% in 1997, to 10% in 2008, and due to high grain prices, will be zero in 2009. Without a view on the permanence of these measures, the long-term benefits of the set-aside policy to diversity and beneficial organisms is unknown. If set-aside is abolished, as seems likely, the Single Payment Scheme and Cross Compliance linked with the Environmental Stewardship Scheme (ESS) aim to give farmers financial incentives to manage land with biodiversity preserving measures in mind. A review (Anon. 2008) of the Environmental Stewardship Scheme set up in March 2005 indicated that the initial take -up by farmers had progressed well and included revised prescriptions for wildlife seed mixtures, skylark plots and over-wintered stubbles, and new twelve metre grass field margins. However the report acknowledges that, owing to the voluntary nature of this scheme, these measures will not be a sufficient response to the complete cessation of the requirement for set-side by all farmers.

The growth of the organic agricultural industry has shown that a section of the public perceives the effects of pesticides on human health and the environment to be serious enough to warrant a change in their purchasing behaviour. The implementation of these policies has then both public appeal and supports the pragmatic principles of sustainability in reducing chemical inputs, minimising soil erosion and preserving biodiversity.

A practical example of the benefit in such changes in practice is seen in the case of Integrated Pest Management (IPM). IPM, which encompasses the use of cultural, biological and chemical control of crop pests, has been applied in some form for over a century although the term was formalised in definition in response to the liberal use of pesticides in the 1940s and 1950s (Begon, Harper *et al.* 1996). Over-use of pesticides, in removing natural biological control, allows pest numbers to then grow unchecked (pest resurgence) particularly when pests have attained resistance or multiple resistance to several pesticides Non pests may also attain pest status through the removal of natural predators (secondary pest outbreak). IPM requires pesticides to be sprayed only when damage from pests reaches an economic threshold i.e the cost of the perceived yield loss exceeds that of the pesticide application. The natural control of pest species by predators and parasitoids occurring in the same habit is important to keep yield losses within this threshold (Greig-Smith 1993). The action of beneficial species which minimise the uneconomic application of pesticide assists in achieving the desired overall reduction in pesticide usage.

Policies and changes in practice which reduce the detrimental effect of intensification on beneficial invertebrates contribute to reducing reliance on pesticides for pest control To better tailor policies towards the preservation of beneficial invertebrates it is important for scientific investigations to discover more about their autecology and the efficacy of measures taken to encourage their persistence in the environment.

1.2.2 Agriculture and arthropods

The land area currently farmed in Britain is 71%, with arable crops (e.g. wheat and barley) and bare fallow accounting for 42%, and temporary ley and permanent ley together a further 43%. (DEFRA statistics for 2007 at http://www.defra.gov.uk/esg/work_htm/publications/cs/farmstats_web/default.htm). Apart from rough grazing land on less fertile soils, all farmed land is compartmentalised into bounded fields of varying size and shape. In the inception of enclosing discrete patches of land, the prime function was to control the movement of livestock (Grigg 1989). To the modern arable farmer, reliant on mechanisation for cultivation of single crops, these boundaries often have been perceived as a hindrance, and frequently result in losses of hedgerows and increased field sizes. The current rate of hedgerow removal however may now be in balance with that being created (Robinson and Sutherland 2002) and overall the field system remains an established feature of the UK's agricultural landscape.

For invertebrates, fields comprise a shifting mosaic of available habitats (Thomas and Jepson 1999). Individual crops in fields represent different stages of secondary succession, disturbed periodically by farm practices and operations differing in magnitude and effect. The abundance of invertebrates present in a field may be affected to differing degrees by livestock grazing and farming operations such as spring sowing, harvesting or pesticide applications. Similarly as crops grow, mature and senesce they change in suitability for both pests and beneficial invertebrates alike. The early successional environment provides a habitat where competition and predation are reduced (Begon, Harper *et al.* 1996). These resources are ephemeral but also highly predictable (Wissinger 1997). An ephemeral habit selects for those species capable of completing their generation within its duration. In habitats where duration is close to the generation time, species exploiting such resources typically have a high capacity to

disperse, enabling them to move quickly to alternative habitats before the old habit becomes too hostile (Southwood 1977). Such species are typically described as having r-strategist traits (MacArthur and Wilson 1967) such as being small and highly fecund with rapid development. Even mating may be consequentially brief (Maes, Vanacker *et al.* 2004) The source areas for species colonising crops annually are habitats in which they can successfully over-winter These habitats are typically perennial or those with relatively lower disturbance. Wissinger (1997) has described species moving between perennial and predictably ephemeral habitats as 'cyclic colonisers'. These do not exhibit exclusively r-strategist traits For example, in unstable habitats, where mortality is not density-dependant, an r-strategist may be expected to allocate more resources to reproductive effort and increase the number of dispersing individuals. Cyclic colonisers however also disperse to permanent habitats where they delay reproduction and enter a physiological state that increases survival, a trait which may be regarded as K-strategist in nature (Wissinger 1997).

Many beneficial carabid beetles exhibit a cyclical colonisation pattern (Lee and Landis 2002; Thomas, Sotherton *et al.* 1992) examples being the carabid beetles *Bembidion lampros* Herbst, *Pterostichus cupreus* L , *Agonum dorsale* Pontopidan, and *Demetrias atricapillus* L which overwinter in field boundaries (Sotherton 1984; Wallin 1986) Linyphiid spiders common in crops, such as *Tenuiphantes tenuis* (Blackwall) (Sunderland 1996) and *Erigone atra* (Blackwall) also overwinter in perennial habitats (De Keer and Maelfait 1988b) Beetles moving between habitats may either travel cursiorally or, if able, may fly Spiders too may walk, but a behaviour observed in many species is that of 'ballooning' where the silk producing capacity of the spider is utilised for the purpose of aerial dispersal.

1.2.3 The nature of aerial dispersal by spiders; ballooning

To disperse by ballooning, a spider releases silk from the spinnerets into moving air. The silk then effects a frictional drag which, in exceeding the gravitational pull on spider, enables it to become airborne or 'balloon'.

Prior to ballooning, a spider's first response is to climb (Suter 1999). Seeking an elevated location assists take-off by allowing the spider and silk to be positioned where air is in motion (Suter 1999). Compared to the action of wings, the released silk does not generate lift and from take-off the spider is in effect falling. However when the upwards vertical movement of the air exceeds the terminal velocity of the spider, the spider gains height (Suter 1991).

Two methods of take-off are commonly used; 'suspended' and 'tiptoe'. In suspended take-off the spider, for example positioned on a blade of grass, drops from the leaf on a length of silk and remains suspended in air. The spider then releases another longer length of silk which, in being dragged by the air, swings the spider from the suspended orientation towards the horizontal whereupon the supporting thread is cut or breaks (Bell, Bohan *et al.* 2005) allowing the spider to be carried away in the air current. Tiptoe take-off describes the spider's habitat of standing on the ends of the tarsi whilst raising the abdomen prior to releasing silk into the air. This characteristic posture ensures the silk is released freely into the air and away from the substrate. Some spiders such as linyphiids employ both methods whilst others, particularly more primitive spiders, only perform the suspended take-off behaviour (Bell, Bohan *et al.* 2005).

Ballooning occurs at wind speeds below 3 m/s (Vugts and Van Wingerden 1976). Low wind speeds together with non-ideal convection are thought to more likely represent

conditions where a balance between convective and lateral air movement exists such that a spider's gain in height is more effectively translated into distance travelled from the take-off point (Reynolds, Bohan *et al* 2007) Spiders can potentially balloon over large distances. Modelling has indicated that given suitable weather conditions a spider can travel 30 km in six hours (Thomas and Brain 2003). The probability of travelling such distances is however relatively small and most flights are thought to occur near to the ground and cover only a few metres (Thorbek, Topping *et al* 2002).

Ballooning is termed a 'passive' dispersal mechanism in that once airborne the distance travelled, the direction, and the location of the landing site cannot be controlled Such dispersal, reliant on atmospheric processes, obviously presents a risk of spiders being carried into adverse environments where survival and escape is compromised (Thomas and Jepson 1999) An initial model describing the behaviour of silk attached to the spider when airborne (Humphrey 1987) suggested that a spider may be able to exert a degree of control in its fall rate by altering the silk length (Humphrey 1987) or through changes in its posture (Suter 1999) Recent studies however have shown that air turbulence effectively negates any alteration of silk length by convoluting the silk fibre whilst the spider is in flight thereby altering the terminal velocity beyond the spider's control (Reynolds, Bohan *et al* 2007).

Given favourable conditions, ballooning may begin between one to four hours after sunrise (Vugts and Van Wingerden 1976). For spiders living within the stable air of the vegetation layer, wind speeds may be undetectable and alternative variables could therefore initiate pre-ballooning behaviour (Vugts and Van Wingerden 1976). Environmental conditions which may be significant are cold nights followed by sunny days (Bristowe 1939), similarly, cold periods followed by a steep rise in temperature

over a few days (Duffey 1956), vibration indicating windspeed, low humidity, and light levels (Vugts and Van Wingerden 1976; Weyman 1993). Covariation of such variables however can make it difficult to assess their individual influence.

A number of different factors have also been implicated in the variation in ballooning motivation between individuals of the same species. Temperature experienced during development (Bonte, Deblauwe *et al.* 2003), hunger (Weyman, Sunderland *et al.* 1994), infection by bacterial endosymbionts (Goodacre, Martin *et al.* 2009) and possibly localised conditions and genetic isolation (Bonte and Lens 2007; Thomas, Blackshaw *et al.* 2003) are thought influential. Differences in the sex ratio of ballooning linyphiids have also been observed (Duffey 1956; Thomas and Jepson 1999) and there is evidence that ballooning occurs more frequently in the smaller, adult males (Plagens 1986). Variation is also seen between species and families. Whereas many spiders balloon only as immatures, others also frequently balloon as adults, particularly those species which are relatively small in mass.

1.2.4 Strategies of spiders on agricultural land; dispersal and 'bet-hedging'

Although spiders moving between crop and non-crop habitats can be termed cyclic colonisers, this model does not describe their generalised dispersal and distribution in the landscape. Many spiders commonly found in crops also complete their lifecycles in more perennial habitats such as pasture or semi-natural and natural grassland, which are typically disturbed to a lesser degree (Schmidt and Tscharntke 2005b). Some cyclic colonisers also display polyphenic traits, such as apterous morphs in the reproductive period and winged morphs for dispersal to over-wintering habitats, as is often observed in aphids (Braendle, Davis *et al.* 2006). Similarly pond skaters (Gerridae) living in

seasonal habitats exhibit both polymorphic and seasonally polyphenic differences in dispersal ability (Bilton, Freeland *et al.* 2001). In contrast, spiders do not exhibit morphological changes associated with enhanced dispersal either during or between generations. Furthermore, when resources are spatially discrete, as in a particular food plant or a water body, it is advantageous to have wings to provide some degree of directional control. In the absence of wings, spiders dispersing by passive ballooning are unlikely to quickly locate a specific isolated resource although generic changes in vegetation structure could arguably be located by a spider requiring a certain vegetation physiognomy for web building Spiders are also generalist predators which widen the resources available to them if other factors are not limiting They therefore may be able to tolerate a greater range of habitats than that provided solely by the field environment For spiders found in crops, the term 'cyclic coloniser' could be more usefully applied in the context of the agricultural environment, or for biological control purposes rather than as a specific behavioural strategy.

Spiders which occur in high abundance in crops and pasture may be better described as eurytopic in nature (Bonte, Vandenbroecke *et al* 2003) but showing adaptations particularly suited to the variety of early successional grassland habitats that agricultural land provides Such habitats may reflect ancestral grassland habitats disturbed periodically by grazing herbivores (Bell, Bohan *et al* 2005) In this ancestral habitat, the dispersive tendency would be positively selected for if the risk of dispersing was lower than that of remaining in situ Each strategy however represents different cost and benefits. The cost of dispersal could be predation en route, inability to locate a suitable site or mate, landing in a hostile environment (e g. the sea) or experiencing adverse meteorological conditions The advantage of dispersal is escaping the disadvantages of staying in situ, such as avoidance of mortality through trampling, declining resources

through disturbance of vegetative structure or senescence, lower prey availability, avoidance of increasing numbers of predators, parasites, pathogens, and, in dispersing, the potential of finding a new location with lower competition and a lower incidence of mortality-causing factors. For species living in localised or stable habitats the costs of dispersing are often higher than if an individual remains with the parent population (den Boer 1990). However for species living in unstable habitats, a high dispersal tendency is retained owing to the increased turnover of local (meta) populations relative to species living in stable habitats. This prevents natural selection from significantly decreasing dispersal power i.e. no isolated, stable population exists in which dispersal can be selected against and the successful formation of new colonies founded by dispersal then actively selects for this trait (den Boer 1990).

As far back as the 17thC it has been recognised that the months of autumn are associated with the apparent synchronised or 'mass dispersal' of spiders occurring on calm days with fair weather (Blackwall 1827; Parker, Harley *et al.* 1992). Linyphiids, small spiders which disperse as adults and immatures, are typically prevalent in such dispersal events (Bell, Bohan *et al.* 2005). That this behaviour coincides in timing with the movement of some insects into non-crop habitats may imply that similar stimuli promote mass dispersal in spiders. For insects, pre-migration changes are often stimulated by photoperiod and/or temperature (Chapman 1998; Gullan and Cranston 1994; Harada, Inoue *et al.* 2003). However, although photoperiod and temperature are known to influence timing of dormancy, ovipostion, and development in spiders (Cloudsley-Thompson 1987; Kurihara 1979; Schaefer 1977), at present there is no definitive relationship between seasonally-related environmental factors and dispersal. Numbers of spiders found dispersing do though reflect changes in ground population density (Weyman, Jepson *et al.* 1995). As described in *Section 1.2.3*, dispersal by

ballooning is inhibited by wind speeds above 3 m/s (Greenstone 1990; Richter 1970; Vugts and Van Wingerden 1976, Wingerden van and Vugts 1979) Days with low wind speeds are associated with increased ballooning activity (Wingerden van and Vugts 1979), and the combination of high ground densities in autumn may be synergistically responsible for increased dispersal in autumn months. Dispersal triggered by harvesting and declines in habitat quality through senescence (Thomas and Jepson 1999) may also concentrate numbers in less disturbed fields or non-crop habitats (Thorbek and Bilde 2004) which may increase ballooning numbers locally.

Despite more active dispersal in the autumn, low densities in harvested and tilled fields may persist (Dinter 1996) through lower temperatures ceasing reproductive accruement, which accounts for the largest increase in density during the crop growth period (Sunderland and Topping 1993) Low densities could also be attributed to the absence of vegetative structure for web building species (Alderweireldt 1994) and low prey densities Food limitation (Bonte, Deblauwe *et al* 2003; Weyman and Jepson 1994) has been shown to increase dispersal tendency and similarly, spiders are seen to remain longer where prey availability is greatest (Weyman and Jepson 1994). During cold months spiders are known to move deeper into the vegetation layer and into grass tussocks (Aitchison 1984; Schaefer 1977) and so a preference for denser vegetation may be evident The movement of spiders to perennial habitats could be then described as redistribution of individuals partly through crop disturbance, a lower affinity for bare ground and a preference for denser vegetation.

In the absence of sensitivity to seasonally specific exogenic factors, anthropogenic disturbance would appear to be the initiator for this seasonal shift in habitat type However whilst motivation may be increased through hunger, disturbance and habitat

change, spiders are also found to balloon throughout the year, outside of the period of major farm operations. An explanation for this behaviour (Weyman, Sunderland *et al.* 2002) is the adoption by spiders of a mixed Evolutionary Stable Strategy (ESS) (Maynard-Smith 1974; Maynard-Smith 1976).

The mixed ESS is an evolutionary response to the unpredictability of disturbance and dispersal. Propensity to balloon in individual spiders is not observed to vary on a seasonal basis (Weyman, Jepson *et al.* 1995), and so low wind conditions can be exploited potentially over the whole year. The propensity to balloon amongst individuals does however vary on a daily basis (Weyman and Jepson 1994). Weyman *et al.* (2002) describe this mixed or random strategy as a form of 'bet-hedging' against the risks of dispersal and risks of staying in situ where a constant expression of either alone would prove of greater risk than a combination of both. This balance may be shifted towards ballooning if particularly suitable convective conditions are evident or alternatively if a uniformly acting exogenic factor such as temperature makes the probability of dispersing greater for all (Bell, Bohan *et al.* 2005). Linyphiid species (e.g. *Oedothorax* spp. and *Erigone* spp.) also show differing frequencies of ballooning (Thomas and Jepson 1999) and so the probability distribution of ballooning frequency and threshold values relative to wind speed or other conditions may differ between species.

Linyphiids balloon as immatures and adults. As the reproductive capacity of female spiders is separated into several eggsacs and females are able to store sperm, then a risk spreading strategy is also applicable to the distribution of eggsacs between locations. The likelihood of field scale disturbance destroying all the reproductive effect of a

spider can therefore be minimised if eggsacs can then be laid in a number of locations over the landscape scale

1.2.5 Spiders common on agricultural land

In the UK the dominant spiders found in crops belong to the family Linyphiidae (Nyffeler and Sunderland 2003). Only a small proportion of the 267 species known to occur in Great Britain and Ireland (Roberts 1993) predominate on farmland In an agricultural context, and for ease of reference, such spiders are termed 'agrobiont' (Luczak 1979; Samu and Szinetar 2002) As is typical of the family, agrobiont linyphiids are relatively small spiders with adult body lengths of approximately 2 mm (Roberts 1995). This small size is of significance in aerial dispersal, assisting take-off and increasing dispersal distance (Suter 1991) Life histories are synchronous with the major crop growth periods (Toft 1989) Warm temperatures produce fast developing summer generations with colder temperatures inhibiting reproduction and growth in a single over-wintering generation Agrobiont linyphiids are typically eurychronous i e they do not reproduce during a defined period and may extend reproduction to more generations given favourable temperatures (Schaefer 1977). Over-wintering may be undertaken at various stages of development although rarely in the eggsac (Thorbek, Sunderland *et al.* 2003). As reproduction is temperature dependant, numbers of generations observed in north european agrobiont linyphiids vary, although for most species a bivoline or multivoline lifecycle is typical. Determining generation times in crops can be difficult as senescence may lead to emigration (Dinter 1996; Thorbek, Sunderland *et al* 2003) with evidence of further generations being suppressed by farm operations (Dinter 1996, Topping and Sunderland 1998).

The family Linyphiidae is divided into two subfamilies; Erigoninae and Linyphiinae. Of the erigonids, *E. atra* has been recorded as having one generation in winter wheat in Germany (Dinter 1996), two in heavily grazed pasture in Belgium (De Keer and Maelfait 1988b) and four generations in winter wheat in the southern England (Thorbek, Sunderland *et al.* 2003). At the same site only one generation of *Oedothorax fuscus* (Blackwall) was recorded although phenological modelling from temperature dependant development rates indicted that more were possible. Regulation of development by photoperiod has been suggested for this species (and also *Oedothorax retusus* (Westring) (Schaefer 1977)) although relative early emigration from the crop suggested that other factors could be involved (Thorbek, Sunderland *et al.* 2003). Two generations of *O. fuscus* were observed in heavily grazed pasture in Belgium (De Keer and Maelfait 1987b).

Of the Linyphiinae, generations of *T. tenuis* are less clearly defined as they show degrees of overlap (Topping and Sunderland 1998). Although a bivoltine life cycle has been suggested (De Keer and Maelfait 1988b), three hatching peaks have been recorded in UK cereals (Sunderland, Topping *et al.* 1996). *Bathyphantes gracilis* (Blackwall) is also described as bivoltine (Schaefer 1977) but was found to have a unimodal abundance although a fast developing summer generation may have been difficult to distinguish (Sunderland, Topping *et al.* 1996).

At 18 °C, eggsac development in agrobiont linyphiids takes between 13-18 days (Thorbek, Sunderland *et al.* 2003). Differences between species are such that fast developers at low temperatures tend to be slowest at higher temperatures (Thorbek, Sunderland *et al.* 2003). For example, *T. tenuis* has a relatively lower reproductive response to high temperatures (Thorbek, Sunderland *et al.* 2003) although reproduction

is extended more into cooler months than in other linyphiids (Topping and Sunderland 1998). For *T. tenuis*, fed *ad libitum*, a mean of 3.3 eggsacs in wild-caught females was observed with a total fecundity per individual of 77.2 eggs at 15°C. (Sunderland 1996) Similar values have been observed for *O fuscus* at 15°C with 3 eggsacs being produced with an average total fecundity of 66 eggs At 20°C the number of eggsacs rose to an average of 8 7 with an average total fecundity of 213.7 (De Keer and Maelfait 1987a) Eggsac development rate of *O.fuscus* is inhibited by high temperatures, decreasing between 23 °C and 29 °C (Thorbek, Sunderland *et al.* 2003). A slightly higher but similar reproductive rate to *O fuscus* is observed for *E. atra* at 20°C (De Keer and Maelfait 1988a) Diet is seen to markedly influence numbers of eggsacs and total fecundity, both regarding prey quantity and quality (De Keer and Maelfait 1987b, Sunderland, Topping *et al* 1996), although egg weight is not affected in *E atra* (De Keer and Maelfait 1988a). *Erigone atra* is more efficient at converting food to eggs than *O. fuscus* and might therefore be better at tolerating low prey availability in recently disturbed habitats (De Keer and Maelfait 1988a).

Eggsacs are laid in higher vegetation, senescing leaves or cracks in the soil (Bell, Johnson *et al.* 2002; De Keer and Maelfait 1987b; De Keer and Maelfait 1988b) After hatching, development to maturity of *T tenuis* takes between 14 to 53 days depending on the month laid and the typical temperatures experienced. At 20°C, *O. fuscus* females take approximately 24 days to mature with males developing faster in around 19 days (De Keer and Maelfait 1987a) At 20°C, *E. atra* (sex not defined) takes approximately 20 days to reach maturity (De Keer and Maelfait 1987a)

Although agrobiont species share similar life histories, their morphology and behaviour are generally distinct. Body form differs between the two subfamilies with erigonids being smaller and more compact in form with shorter legs. Common Erigoninae include *E. atra*, *Erigone dentipalpis* (Wider) (coexisting with *E.atra* in the same habitats), *O. fuscus*, *Oedothorax apicatus* (Blackwall) (not in the southwest UK) *O. retusus*, *Milleriana inerrans* (O.P.-Cambridge) and *Meioneta rurestris* (C.L.Koch). Erigonids make small webs in depressions in the soil or in the case of *Oedothorax* spp., hunt cursorially (Alderweireldt 1994) but utilise webs for moulting and mating (Maes, Vanacker *et al.* 2004). Male erigonids often have elevated and bizarrely shaped head regions which are thought to have significance in mating and mate selection (Maes, Vanacker *et al.* 2004).

Members of the Linyphiinae have less compact bodies and longer legs. Common species of this subfamily are *T. tenuis* and *B. gracilis*. Whereas for *Erigone* spp., webs are not vital for prey capture, both *T. tenuis* and *B. gracilis* use their webs exclusively (Alderweireldt 1994). Webs are usually made above the ground, supported by surrounding vegetation although deep depressions in the soil can be utilised (Samu, Sunderland *et al.* 1996). *Tenuiphantes tenuis* show competition for webs but also tolerance of occupancy of nearby web sites (Samu, Sunderland *et al.* 1996). Webs of *T. tenuis* are abandoned after less than two days in a randomised manner which is thought to be a risk spreading strategy increasing the dispersion of ovipostion sites (Samu, Sunderland *et al.* 1996). Members of both subfamilies appear to be able to locate webs to maximise prey availability (Harwood, Sunderland *et al.* 2003).

Other common spiders found in crops are those belonging to the family Lycosidae (wolf spiders). Dominant lycosids are usually from the genus *Pardosa* Lycosids are univoltine and disperse aerially as immatures Hunting and local dispersal is usually cursorial and aerial dispersal is more likely in generalist species than specialist species. (Bonte, Vandenbroecke *et al* 2003).

Outside the UK, lycosids are seen to dominate in some regions although differing sampling methods (pitfall trapping or suction sampling) may distort data on community structures being biased either towards epigeic or epiphytic species (Standen 2000). In a meta-analysis of spiders present in arable (cereal and alfalfa) and natural grassland in Hungary, Samu and Szinetar (2002) found in order of highest abundance, the lycosid *Pardosa agrestis* (Westring), the linyphiids *M rurestris* and *O. apicatus* and the tetragnathid *Pachygnatha degeeri* Sundevall. As their presence was almost ubiquitous in all arable situations, they were described as 'core agrobionts' These species were not seen as generalists as they were distinctly dominant in agricultural settings as opposed to natural grassland Schmidt and Tscharntke (2005b) argue that abundance is more important than dominance owing to the overall variation in spider densities, and a study in Germany found substantial numbers of agrobiont species in perennial habitats (grassland and fallows), their high dominance in arable fields being related to a corresponding low density of other species

In Switzerland spiders of the families Linyphiidae, Lycosidae and Tetragnathidae were dominant on agricultural land (Nyffeler and Benz 1988, Öberg, Mayr *et al* 2008). Linyphiids were also the dominant spiders found ballooning (Blandenier and Furst 1997).

In North America, studies on spiders have mostly been conducted in southern latitudes. Differences between Europe and the US are likely to be climatically related and communities display a more complex guild structure not dominated by linyphiids. Cursorial hunters feed on a broader range of prey and densities are far lower (0.02 to 14 per m^2) than those described for UK studies (2 to 600 per m^2) (Nyffeler and Sunderland 2003).

1.2.6 Spiders as beneficial organisms

Fast population growth exhibited by agrobiont linyphiids make them good candidates for biocontrol in annual cropping systems (Thorbek, Sunderland *et al.* 2003). Linyphiids may be active at low temperatures and migrate into fields, or survive farming operations (Sunderland, Fraser *et al.* 1986b; Thorbek and Bilde 2004) to be present in the crop before specialist predators. Predation on aphids in the early crop growth stage is seen as important in suppressing subsequent aphid population development when predator to pest ratios are favourable (Edwards, Sunderland *et al.* 1979; Holland and Thomas 1997). Linyphiids are predacious on cereal aphids *Rhopalosiphum padi* (L.) and *Sitobian avenae* (Fab.) (Nyffeler and Benz 1988). *Rhopalosiphum padi* in particular is a efficient vector of the barley yellow dwarf virus (Dixon, Carter *et al.* 1982). Sunderland *et al.* (1986a) found that for linyphiids, aphids were the second most frequently caught prey after Symphypleona collembolans.

Birhofer *et al.* (2008), in comparing the feeding guilds of web and cursorial spiders, found that cursorial spiders limited the growth rate of the grain aphid *S. avenae* at low aphid densities. Web builders were seen to have no effect suggesting that this guild may have limited predation. However it was acknowledged that body mass of this group is

lower than lycosids and they occur at higher densities Indeed densities for linyphiids in the enclosure were equivalent to 15.7 per m^2 whereas densities during the main growth period in wheat may be as high as 600 per m^2 (Nyffeler and Sunderland 2003; Vickerman 1992) The enclosure used in the study could also have reduced aphid mortality by the exclusion of rainfall Rainfall along with wind may increase the fall rate of aphids from tillers (L Winder pers. comm) thereby increasing numbers caught in webs Clough *et al* (2005) and Oberg (2007) found that cursorial spiders (lycosids) also have a distinct edge effect and occur at lower densities in field centres compared to *Oedothorax* spp and *E atra* However in the Clough study, both linyphiids were less abundant at the field edge possibly due to competitive or intraguild predation from lycosids Their relative presence in different areas of the crop could be complementary from a biocontrol perspective

In laboratory experiments Mansour and Heimbach (1993) found *E atra* to be the most effective predator of the aphid *R. padi* on winter wheat, reducing population development by 58%. Adults and immatures of the lycosids, *Pardosa agrestis* (Westring) reduced population development by 52 4% and 41 7% respectively *Tenuiphantes tenuis* was found to reduce population development by 34%. Despite this relatively low reduction, abandoned webs of *T tenuis* (Samu, Sunderland *et al.* 1996) may constitute an additional control for pest species in catching and retaining pests even when the web is not occupied (Nentwig 1987; Sunderland 1999) Sunderland *et al* (1986b) found that sheet-webs covered half the surface area of a winter wheat field by early August

Spiders are observed to kill more prey than they consume (Mansour and Heimbach 1993; Sunderland 1999). Regarding *R. padi*, this superfluous killing response could be

related to its poor nutrient quality such that first instar *E. atra* and *Pardosa amentata* (CL.) are unable to complete development when fed on *R. padi* exclusively (Toft 1995b). Spiders then may kill excess aphids but remain unsatiated (Sunderland 1999). An aversion to aphids as prey has been observed in the lycosid spider *Pardosa prativaga* (L.K) (Toft 1997). Tolerance to aphids may be enhanced by spiders feeding in field margins prior to migration into the crop (Beck and Toft 2000).

As generalists, spiders can maintain their populations by feeding on alternative prey when pest densities are low. Generalist predators however display inter- and intraguild competition and cannibalism (Samu, Toft *et al.* 1999) which reduce their biocontrol potential. In a review of competition between spiders, Marshall and Rypstra (1999) concluded that increased spider diversity could lead to greater competition, but also that feeding on other spiders was a potential useful alternative food source (but see Östman, Ekbom *et al.* 2001 below) and a more diverse spider fauna would occupy more niches thereby potentially increasing their effectiveness. Increasing spider diversity may also have benefits for controlling pests over a longer period of time as individual species may be more effective during different periods of the year (Riechert 1999).

1.2.7 Interaction between beneficials and landscape and field scale factors

With the recent emphasis on increasing biodiversity in agricultural habitats, many studies have focused on the interaction between features in the landscape known to promote biodiversity and the abundance and efficacy of beneficial predators.

A study in Sweden (Östman, Ekbom *et al.* 2001) on the effect of natural enemies on the aphid *R. padi*, found that landscapes with abundant field boundaries and perennial crops

were associated with low aphid establishment in cereals. Organic farm practice was seen to improve the impact of natural enemies compared to conventional methods High predation rate however was associated with low heterogeneity on the medium scale (400 x 400 metre squares), and predation also improved when arable areas were contiguous. Natural predators were thought to spend more time in alternative habitats in high heterogeneity areas thereby reducing their biocontrol potential. Although more effective at establishment, the impact of predation in organic systems on the growth rate of aphid populations, decreased during the aphids' exponential growth stage to that observed in conventional systems, possibly due the presence of alternative prey The overall effect was however a positive biocontrol impact in high perimeter to area ratio sites with perennial habitats

Oberg *et al* (2008) found that activity-density of *O apicatus* and *E. atra* were not related to the total length of field boundaries although *M. ruretris* was seen to be positively influenced by boundary length in spring The lack of further increase in activity-density indicated that, prior to the beginning of the study in March, linyphiids had already migrated into the fields or were present in the crop over winter and no further ingress had occurred thereafter. Activity-density of lycosids did increase over time indicating gradual cursorial movement into the crop. Abundance was not related to boundary length although diversity did increase

Schmidt *et al* (2008) found that an increase in non-crop habitats (grassland, fallow and forest) had a positive effect on the activity-densities of most spiders sampled Some species found abundantly in annual crops (*T. tenuis*, *Pachygnatha clercki* Sundevall, *Porhomma* spp. and *O apicatus*) were however negatively associated with non-crop

habitats in a region where a high proportion of the landscapes studied had less than 30% arable land.

These studies appear to indicate that for beneficial predators boundary length may have a positive overall effect but for agrobiont spiders capable of dispersing long distances, local boundaries may not be so relevant. This is also supported by Schmidt and Tscharntke (2005a), who found that correlations between sheet-web spider abundance in winter wheat and non-crop habitats were most distinct at scales of 1 to 3 km indicating that these features were more important over the wider landscape. The Schimdt *et al.* (2008) study however emphasises the importance of the arable crop as a primary habitat for some species; whilst an increasing proportion of non-crop habitats may be be beneficial for over-wintering, when this exceeds a certain threshold the lack of primary arable habitat may depress abundance of common arable species.

As suggested in the Östman *et al.* (2001) study, increasing abundance of beneficials in the margins will be unproductive if non-crop habitats are preferred or low dispersal means their migration into the crop is poor (Riechert 1999; Sunderland and Samu 2000). Heidger and Nentwig (1989) found that the spider *Dictyna arundinacea* (L.) was an effective predator of crop pests but only at high densities produced by artificial introduction. This species builds cribellate webs on the ears of wheat and therefore is placed where many pest species are active (thrips, aphids). However, lack of migration from weed strips into an adjacent wheat crop and *vice versa* dramatically reduced the numbers returning to the crop in the following spring. Similar results were also seen in alfalfa (Samu 2003) where strip management increased spider abundance and diversity but did not elevate abundance in the crop. It was thought that more diverse methods of introducing heterogeneity into the crop may increase migration.

Sunderland and Samu (2000) describe strip management and intercropping as 'aggregated diversification' and reviewed studies indicate a positive effect on spider abundance in only 33% of cases. Reduced tillage, mulches, weediness and undersowing are examples of 'interspersed diversification'. These practices are seen to be more effective, increasing abundance in 80% of studies Naturally occurring grass weeds are seen to increase spider abundance in barley plots (Vickerman 1974), and higher densities of spider are observed to occur in weedy areas within winter wheat (Topping and Sunderland 1994). Diversity of spiders was not however observed to differ between conventional fields and organic fields with significant weed cover (Clough, Kruess *et al.* 2005). In this case, weed harrowing in organic fields was suggested as a possible factor in reducing spider populations Significant direct mortality has been previously recorded from this operation (Thorbek and Bilde 2004).

Encouraging spiders known to already successfully migrate into crops is an obvious measure for improving biocontrol. As mentioned previously, the correct balance of crop to non-crop habitat appears important for agrobionts Set-aside, in being structurally similar to cereals, provides an ideal non-crop habitat, and the physiognomic similarity of crops and non-crop habitats is seen to be important for increasing migration into crops (Sackett, Buddle *et al.* 2008) In modelling the influence of non-rotational set-aside on *T. tenuis*, it was shown that presence of set-aside significantly increased abundance of spiders in crop areas (Topping and Sunderland 1994b)

The timing of management interventions on field margins has been shown to affect abundance of *T. tenuis*. Cutting margins, particularly in summer months was seen to have a greater and more persistent effect than cutting in spring (Bell, Johnson *et al* 2002). The degree of direct mortality from this management is not known but Thorbek

and Bilde (2004) have suggested that spring mowing of grass for silage could have a positive effect in redistributing beneficial spiders into nearby crop areas.

1.3 Long-term trends in spider populations

As the last sixty years have brought considerable change to the agricultural industry, the future at the beginning of the 21st Century could be as changable with potentially challenging scenarios emerging, the long-term effects of which are uncertain. Rises in food prices, the loss of set-aside, increased planting of biofuel crops, and the direct and indirect effects of climate change may all have significant implications for agriculture, spider populations and biological control.

Agribiont spider populations are sensitive to landscape scale influences, and populations may reflect changes in land-use and practice over the wider area. In attempting to assess population change, experiments based on localised sampling with the added limitations of experimental design and execution make it difficult to –

a) accurately evaluate the effect of landscape processes on local populations whilst accounting for local-scale factors

b) explore the effect of changing scenarios of climatic extremes and variables and subsequent effects on non-crop habitats, and the diversity and coverage of crops grown which may have no allegories in the existing landscape

c) extrapolate over larger spatial and temporal scales

In an effort to address these problems, computer modelling can be used to simulate both spider behaviour and the effect of landscape processes and climate mediated dispersal on the persistence and trends in spider populations. Halley, Thomas and Jepson (1996) produced a simple model describing estimated dispersal and reproductive rates in a periodically disturbed linear landscape of five habitat types It was found that given a certain temporal and spatial pattern of hazards and resources, a particular dispersal strategy leads to a particular population size Too much or too little dispersal however leads to regional extinction and therefore variation in life history and dispersal strategies of individual species lead to different population sizes in the same landscape (Halley, Thomas *et al* 1996). A model of spatial population dynamics for *T tenuis* (Topping and Sunderland 1994a) found that despite considerable disturbance, survival of metapopulations persisted through emigration although disturbance outside of the reproductive period made metapopulation extinction more likely An individual-based model (Topping 1999; Topping and Sunderland 1994b) has shown rather counterintuitive effects where in the event of minimal dispersal, large field sizes increase populations relative to smaller fields, owing to the negative effect of high densities on growth curves Modelling has also indicated the positive benefits of set-aside for *T tenuis* (Topping and Sunderland 1994b).

Whilst meteorological and remote sensing data on landscape structure can give baseline information for model parameterisation, data on dispersal behaviour and species specific life histories are more complex and time consuming to acquire. Progress has been made in modelling dispersal distances (Thomas and Brain 2003), dispersal timing and behaviour when ballooning (Reynolds, Bohan *et al* 2006, Reynolds, Bohan *et al* 2007) and in the development of physical allegories to test model predictions (Bell, Bohan *et al* 2005) Species specific information on life histories is also available for

some common agrobiont spiders (De Keer and Maelfait 1987a; De Keer and Maelfait 1988a; Sunderland, Topping *et al.* 1996; Thorbek, Sunderland *et al.* 2003; Topping and Sunderland 1996).

In order to advance current knowledge, further investigation is required on the interaction between spiders and their environment (Bell, Bohan *et al.* 2005; Weyman, Sunderland *et al.* 2002). Observation and monitoring provide the basis for subsequent laboratory and field manipulation studies which are necessary to understand the plasticity of response to differing biotic and abiotic factors. Experiments and monitoring however always have to operate within the bounds of time and cost, and therefore the development of sampling techniques is vital for improving the accuracy and extent of data collected. More accurate and extensive data should lead to models that have greater power in predicting the fate of populations over a wider range of potential scenarios.

1.4 Experimental aims and objectives

The aims of this study are:-

i To develop and test a trapping method for measuring spider dispersal activity in the field

ii To provide data on species-specific ballooning behaviour in a wind chamber

iii. To compare laboratory results with the timing and frequency of spider dispersal in the field

iv. To assess sampling techniques for measuring ground populations of spiders

v. To describe the seasonal variation of populations of common agriculture species on a mixed-farm

vi. To describe the assemblage structure of common agriculture species in different crop types

vii To assess the effects of farming operations on populations of spiders in different crops types

viii. To test the following hypotheses

- That linyphiid species exhibit different propensities to balloon under laboratory conditions
- That spiders common on farmland exhibit species-species patterns of ballooning activity in the field over time
- That spiders show distinct differences in assemblage structure at the field scale depending on field characteristics relating to crop type
- That farm operations associated with different crop types have different degrees of impact on spider populations

Chapter 2. General materials and methods

2.1 Site description

The work was conducted on the Seale-Hayne Faculty estate farm, formerly the Faculty of Food and Land Use, University of Plymouth. The study area is near the market town of Newton Abbot in the county of Devon in the southwest peninsula of the British Isles. The South West is the most rural region of the British Isles with 80% of land in agricultural use. Production is dominated by pastoral livestock farming (dairy, beef and sheep) with localised pockets of intensive arable production (Anon. 2000).

The farm of 180 hectares (Figure 2-1) is located between the estuary of the River Teign, 6 km to the east, and the Dartmoor National Park 4 km to the west and lies partially on the southern side of Ingsdon hill. The topography is relatively flat to the south being between 60 to 85 metres above sea level, and rises steadily to the north from the central farm buildings to the northern boundary which nears the hill's summit at 182 metres. Fields are mostly in fodder crops and grass leys which provide grazing for 200 head of holstein fresian cows and approximately 500 sheep. Temporary leys are on a seven year rotation with fodder crops rotated every two years. A single field of permanent ley (Bradmores), adjacent to the farm buildings, is used as night pasture for the dairy herd. Fields included in the study were in set-aside, winter barley, winter wheat, maize, temporary ley and permanent ley (Table 2-1). Set-aside is land taken out of normal farm production where management is limited to a single grass cut (topping) in early August and grazing from mid September to mid January. The field Backdown was designated as set-aside a year prior to the study although the field has a previous history of low intensity management and periodic grazing by sheep owing its steep access and

boundary location Along with various graminaceous species, typical plant species found here included common poppy (*Papaver rhoeas* L.), hogweed (*Heracleum sphondylium* L.), field thistle (*Cirsium arvense* (L.) Scop.) and stinging nettle (*Urtica dioica* L). Grass leys were harvested for silage in May and July and set-aside had a single mowing in early August. Typical harvesting times for arable crops were July for barley, August/September for wheat and October for fodder maize

Table 2-1 Fields and corresponding crops included in the study in 2001 and 2002

Field	Abbr (Fig 2-1)	2001	2002
Backdown	BD	set-aside	set-aside
Eastdown	ED	Maize	maize
Pitstones	PS	temporary ley	wheat
Horse Parks	HP	barley	temporary ley
Bradmores	BM	permanent ley	permanent ley
Bigfield	BF	temporary ley	temporary ley
Glazeparks	GP	wheat	wheat

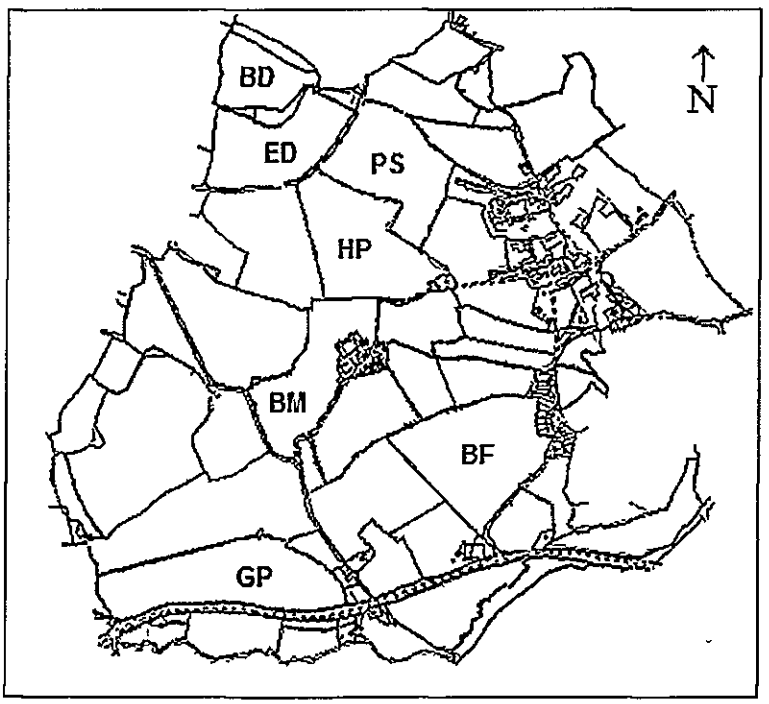

Figure 2-1 Map of estate farm showing fields in which sampling took place (see Table 2-1 for field names and crops) The main farm buildings are situated in the centre of the map adjacent to Bradmores, the Seale-Hayne faculty buildings being to the east

2.2 Sampling techniques

2.2.1 Aerial sampling of spiders

A novel technique developed during the course of this work is described in Chapter 3.

2.2.2 Ground sampling of spiders

Sampling performed for the study detailed in Chapters 5 and 6 utilised the D-vac suction sampler in a variety of crop types although in Chapter 4 a G-vac suction sampler was used for sampling in grass.

2.2.2.1 Background to sampling with D-vac and G-vac samplers

The earliest recorded use of a mechanical suction device is from Hills (1933) who describes a pipette connected to small electric blower fan, used to collect insects from an enclosure. Not until after WWII were larger suction devices developed to sample invertebrates directly from their habitats. One of the earliest machines, described by Dietrick *et al.* (1959), was constructed from war surplus materials and incorporated a heavy petrol engine requiring it to be carried on a mobile mount (Figure 2-2). In a later version, use of a lighter motor enabled the machine to be hand-held. Sampling however still required two people; one to carry the motor and one to sample. Further development led to the motor being mounted on a backpack enabling the sampler to be operated by a single person (Figure 2-3). This device, the D-vac, was the first commercially available suction sampler and is still in production today (manufactured by Rincon-Vitova Insectaries, US). In comparison to the modern version, the D-vac described in Dietrick's 1961 paper is largely unchanged, consisting of a lawnmower-

type, 2-stroke petrol engine, driving an impeller which draws air through a flexible, reinforced, rubberized tube, the front end of which houses the collecting net. Samples are taken by placing the end of the tube over the vegetation and onto the ground (Figure 2-3). Air drawn under and through vents in the sides of the reinforced aperture, dislodges invertebrates which are in turn trapped in the net. The air passes through the net and a wide metal mesh, there to protect the impeller, before being expelled through the exhaust at the rear of the impeller housing.

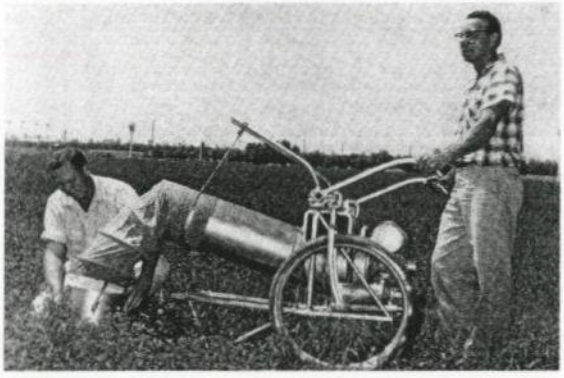

Figure 2-2. An early suction sampler being used to sample aphids and natural enemies from lucerne.

Despite the D-vac having been used extensively as a sampling device in ecological and entomological studies (Borges and Brown 2003), a number of shortcomings have been noted, the most apparent to operators being its weight (Stewart and Wright 1995). The heavy motor and its high centre of gravity present difficulties for sampling on uneven ground and in transporting the equipment to the study site when access by vehicle is not possible. The suction power when using the standard aperture of 0.1 m^2 also has been questioned, in that reliable absolute population estimates may not be achieved, particularly when vegetation is dense (Sunderland and Topping 1995) and target organisms are large or tenacious species living close to the ground (Duffey 1980; Southwood and Henderson 2000). The cost of these units is also expensive being in the order of £1450.

Figure 2-3. The backpack mounted D-vac sampler (model 24) in operation.

An alternative to the D-vac came in the form of the petrol-driven garden vacuum (Figure 2-4), intended for the household market to collect or blow fallen leaves from paths and gardens. The light weight, low cost, ease of modification and high suction power (De Barro 1991; Wright and Stewart 1992), albeit with nozzle diameters smaller than the D-vac's, made for their rapid adoption as primary sampling devices. In most cases the simple addition of a net either secured over the end of the suction nozzle, or installed further down its length is sufficient to convert the 'garden vacuum' into a 'G-vac' sampler.

Although G-vacs and related devices such as the Vortis sampler (Arnold 1994) are now used in preference to the D-vac in many sampling situations, the small size of the collection area is a limitation (Samu and Sarospataki 1995) particularly when sampling in tall standing crops. Increasing the nozzle diameter of G-vacs may lead to a substantial loss in sampling efficiency (Bell, Wheater *et al.* 2000). Although less powerful than the G-vacs, the larger aperture of the D-vac is capable of accommodating taller vegetation particular when fitted with a nozzle extension (Figure 2-4). The extra length of the nozzle allows the whole crop to be covered without damage and prevents the crop pressing against the inside of the net which could impede the airflow.

2.3 Assessing the efficiency of D-vac and G-vac suction samplers

2.3.1 Introduction

The objective of this study was to assess the relative efficiency of each device in sampling spiders from winter-wheat and grass, to determine their suitability for sampling each vegetation type.

2.3.2 Materials and methods

The D-vac sampler used was powered by a 2-stroke Tecumseh petrol engine (98 cm^3, 4.5 bhp). The nozzle was extended by the addition of a 1 metre aluminium tube with a diameter of 36 cm, the sampling area being 1017 cm^2. The G-vac was a converted Flymo BVL-320 garden vacuum (engine size 32 cm^3) with a forty centimetre long voile net secured above the rear flange of the distal section of the nozzle (Figure 2-4). The net was secured using a jubilee clip. A small section of the tube was removed to expose the clip's screw allowing the circular band to be tightened against the inside of the tube, thus holding the opening of the net in place. The elliptical aperture was equivalent to a circle diameter of 12.6 cm and had a sampling area of 125 cm^2.

Figure 2-4. D-vac suction sampler with nozzle extension and modified Flymo BVL 320 G-vac in foreground. The nozzle of the G-vac is divided into two parts with the net being secured inside the distal section by a jubilee clip tightened against the inside.

Sampling took place in temporary ley and winter wheat on the Seale-Hayne Faculty estate farm between January 2004 and September 2004. Samples were taken in the central region of the fields to minimize edge effects. In order to delimit the area to sample, a movable enclosure was made from a circular band of rigid plastic,10 cm in height and 37 cm in diameter, this being slightly larger than the diameter of the D-vac nozzle (0.1 m^2). In order to provided anchor points to ensure the enclosure would sit tight to the surface, four wire pegs were made from 10 cm lengths of 2 mm fencing wire. These were attached to the sides of the enclosure at equidistant points with 5 cm of the wire protruding beneath. The enclosure provided both a guide for the samplers and a barrier to impede movement of spiders out of the area during sampling.

Each month, five replicates were taken by each sampler. In both fields, five marker poles were placed in a line at 3 m intervals. One sample from each sampler was taken at each of the five markers. At each marker the samples from the D-vac and G-vac were

taken either side of the marker pole within the movable enclosure. Each replicate taken with the D-vac consisted of a 10 second placement within the enclosure. For the G-vac, each replicate consisted of ten 1 second placements within the enclosure. The placement of the G-vac nozzle into the enclosure was done in systematic fashion with eight placements round the inner-side of the enclosure and two in the middle. An amount of overlap of the G-vac placements was unavoidable though was thought necessary to cover as much of the area as possible given the incongruent shapes of the nozzle and the enclosure.

Immediately following each 10 second sample, the area was suction sampled for 2 minutes using the G-vac, this being the more powerful device. This was followed by hand-searching until all observable spiders were collected. Sampling efficiency was defined as being the proportion of spiders sampled initially to those remaining and recovered after sampling. In wheat, by June the G-vac could no longer be used to sample the full height of the crop and the ground, therefore, after placing the enclosure over the crop, the wheat was cut to a height of 10 cm before sampling. Although spiders present in the wheat above this height may have fallen into the enclosure, any remaining spiders in the excised wheat were classed as unobtainable by the sampling protocol and therefore not included. Samples were taken each month between January and September with the exception of May in the wheat and August in the temporary ley. Prior to sampling, five height measurements and a visual estimate of percentage vegetation cover were taken within each sampling area.

As some samples suffered desiccation prior to determining class sizes, the length of the carapace was measured instead of the whole body length. The chitinous carapace was less prone to deformation than the softer abdomen and so was a more accurate estimator

of total body length when alive. The carapace lengths used for size classes were 0.2 to 0.5 mm for 'small', 0.6 to 0.9 mm for 'medium' and 1 mm and above for 'large' which constituted mostly adult linphyiids.

2.4 Results

2.4.1 Efficiency of sampling size classes

The G-vac sampler was relatively more efficient in wheat in the earlier months preceding June (Table 2-2) although the low densities of spiders from January to March caused efficiencies to be wide ranging relative to the number of spiders sampled. The D-vac was more efficient in the summer months particularly for small and medium spiders. Samples in August and September were taken after harvesting and the low ratios for these months indicate that the G-vac was more efficient in wheat stubble. Average efficiencies over all months (Figure 2-5) were higher for the G-vac sampler although paired t-tests on arcsine transformed percentages did not indicate significant differences between samplers for either small ($T_{(1,5)} = -1.04$, $P = 0.338$) or medium ($T_{(1,6)} = -0.39$, $P = 0.707$) size classes. Efficiency of sampling the large size class was though significantly higher for the G-vac than the D-vac ($T_{(1,5)} = -2.47$, $P = 0.049$).

Large disparities however were observed between the efficiencies of the G-vac and D-vac in grass (Table 2-3). The predominance of ratios below 1 for virtually all months clearly demonstrates the higher sampling efficiency of the G-vac. For the D-vac a reduction in efficiency is also observed for increasing size classes. In D-vac samples medium sized spiders were sampled with relatively low efficiency and large spiders were not sampled at all. Efficiencies for the smallest size class showed marked variations over the months (Figure 2-5).

Table 2-2 Percentage efficiency of G-vac and D-vac samplers in winter-wheat for three size classes of spiders The ratios refer to the ratio of the 'efficiency' of the 10 second samples of the G-vac and the D-vac i e. the sample relative to the total numbers found For example for January 'small' 50 – 100 equals a ratio D-vac $_{10sec}$: G-vac $_{10sec}$ of 0.5.

Sampler & size class		Month (Wheat) Jan	Feb	Mar	Apr	Jun	Jul	Aug	Sep
G-vac small	N° $_{10\,sec}$	1	0	1	3	14	11	1	47
	N° total	1	0	3	3	18	21	6	72
	% efficiency	100	na	33 3	100	77 8	52 4	16 7	65 3
D-vac small	N° $_{10\,sec}$	1	0	1	10	48	31	3	32
	N° total	2	1	5	14	54	36	22	82
	% efficiency	50	0	20	71 4	88 9	86 1	13 6	39
Ratio	D-vac $_{10\,sec}$ G-vac $_{10\,sec}$	0 5	na	0 6	0 71	1 14	1 64	0 82	0 6
G-vac medium	N° $_{10\,sec}$	0	0	2	2	9	12	17	14
	N° total	1	1	2	2	19	27	34	22
	% efficiency	0	0	100	100	47 4	44 4	50	63 6
D-vac medium	N° $_{10\,sec}$	0	1	3	11	41	11	6	4
	N° total	2	2	5	12	48	23	54	20
	% efficiency	0	50	60	91 7	85 4	47 8	11 1	20
Ratio	D-vac $_{10\,sec}$ G-vac $_{10\,sec}$	na	na	0 6	0 92	1 8	1 08	0 22	0 31
G-vac large	N° $_{10\,sec}$	0	0	2	3	13	14	16	11
	N° total	1	0	2	3	18	20	25	14
	% efficiency	0	na	100	100	72 2	70	64	78 6
D-vac large	N° $_{10\,sec}$	0	0	2	1	17	5	2	3
	N° total	3	0	7	4	29	6	6	9
	% efficiency	0	na	28 6	25	58 6	83 3	33 3	33 3
Ratio	D-vac $_{10\,sec}$ G-vac $_{10\,sec}$	na	na	0 29	0 25	0 81	1 19	0 52	0 42

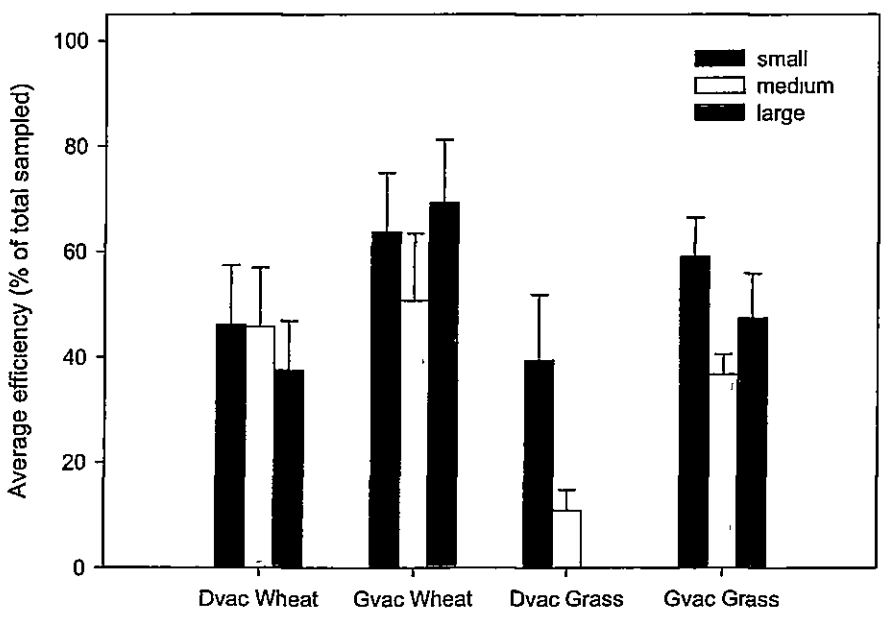

Figure 2-5 Average efficiency and standard errors for size classes sampled from January to September in winter wheat and grass

Of particular note was the relatively high sampling efficiency of 65.5% observed in April, when the grass was at its tallest prior to harvest and when densities of immatures were at their highest. No significant difference between the G-vac and D-vac was observed for the smallest size class ($T_{(1,5)} = -1.53$, $P = 0.176$) although a significant difference was apparent for the medium ($T_{(1,6)} = -7.6$, $P < 0.001$) and large ($T_{(1,6)} = -5.34$, $P = 0.001$) size classes.

Table 2-3. Percentage efficiency of G-vac and D-vac samplers in grass for three size classes.

Sampler & size class		Month (Grass) Jan	Feb	Mar	Apr	Jun	Jul	Aug	Sep
G-vac small	N° $_{10\,sec}$	1	0	1	41	18	14	35	17
	N° total	2	0	3	47	23	27	90	23
	% efficiency	50	na	33.3	87.2	78.3	51.9	38.9	73.9
D-vac small	N° $_{10\,sec}$	0	1	2	38	4	1	12	5
	N° total	1	1	2	58	15	36	31	12
	% efficiency	0	100	100	65.5	26.7	2.8	7.8	41.7
Ratio	D-vac $_{10\,sec}$: G-vac $_{10\,sec}$	0	na	3	0.75	0.34	0.05	0.2	0.56
G-vac medium	N° $_{10\,sec}$	5	2	1	3	4	4	33	15
	N° total	14	4	2	11	11	22	73	48
	% efficiency	35.7	50	50	27.3	36.4	18.2	45.2	31.3
D-vac medium	N° $_{10\,sec}$	2	1	1	0	1	1	2	1
	N° total	11	3	5	6	15	20	79	86
	% efficiency	18.2	33.3	20	0	6.7	5	2.5	1.2
Ratio	D-vac $_{10\,sec}$: G-vac $_{10\,sec}$	0.51	0.67	0.4	0	0.18	0.28	0.06	0.04
G-vac large	N° $_{10\,sec}$	12	4	6	5	5	3	6	5
	N° total	26	4	14	17	8	7	15	32
	% efficiency	46.2	100	42.9	29.4	62.5	42.9	40	15.6
D-vac large	N° $_{10\,sec}$	0	0	0	0	0	0	0	0
	N° total	10	5	1	16	5	7	19	33
	% efficiency	0	0	0	0	0	0	0	0
Ratio	D-vac $_{10\,sec}$: G-vac $_{10\,sec}$	0	0	0	0	0	0	0	0

A Chi-square test was performed to determine whether frequencies of small, medium and large size classes in the 10 second samples were proportional to absolute frequencies. In wheat, no significant differences was seen between 10 second sample and absolute frequencies either for the G-vac ($\chi^2_2 = 2.977$, $P = 0.225$) or the D-vac ($\chi^2_2 = 2.922$, $P = 0.232$). In grass a significant difference was observed for both the G-vac

(χ_2^2 = 13.243, P < 0.001) and the D-vac (χ_2^2 = 49 772, P < 0.001) samplers. In both samplers the frequency of small spiders in the 10 second samples was greater than the expected frequencies The bias to a higher frequency of small spiders was however greater in the D-vac than the G-vac.

For the grass field, regression analysis revealed no significant relationship between grass height on the efficiency of sampling small, medium or large size classes for either suction sampler In wheat, a positive relationship between crop height and sampling efficiency was observed for the D-vac in sampling small (R-sq = 60.7, $F_{(1, 5)}$ = 9.25, P= 0 023) and large (R-sq = 72.8, $F_{(1, 5)}$ = 13.41, P = 0.015) size classes For the G-vac in wheat, height and sampling efficiency are positively related for medium (R-sq = 82.1, $F_{(1, 6)}$ = 27.51, P = 0 002) and large (R-sq = 69 9, $F_{(1, 5)}$ = 11.62, P = 0.019) size classes. In wheat and grass no relationship was observed between efficiency and percentage cover for either suction sampler.

2.4.2 Efficiency of sampling species

In grass the lack of larger spiders sampled by the D-vac is apparent in *B.gracilis*, a relatively small species, being the sole adult spider sampled (Table 2-4). This single species sampled with the D-vac also represents the species sampled with greatest efficiency using the G-vac sampler (27 3% to 80% respectively). For the G-vac, another epiphytic species, *T tenuis*, was also sampled with a relatively high efficiency (66.7%). Epigeal species such as *Oedothorax* and *Erigone* species had lower efficiencies of between approximately 25% and 40% Larger spiders such as the lycosids and the *P. degeeri* had efficiencies of 25% and 50% respectively.

Table 2-4. Efficiency (percentage of total) of 10 second samples using the G-vac and D-vac samplers for species and immatures in wheat and grass.

Species	Grass		Wheat	
	G-vac	D-vac	G-vac	D-vac
Bathyphantes.gracilis	80	27.3	42.1	68
Centrometrita concinna	50	0	--	--
Dicymbium nigrum	20	0	--	--
Erigone atra	39.3	0	53.3	14.3
Erigone dentipalpis	30.8	0	50	0
Lycosa	25	0	100	100
Milleriana inerrans	26.1	0	100	0
Oedothorax fuscus	39.7	0	88.9	70
Oedothorax retusus	25	0	50	0
Pachygnatha degeeri	50	0	60	54.5
Porhomma microphathalmum	--	--	33.3	50
Savignia frontata	0	0	--	--
Tenuiphantes tenuis	66.7	0	52.6	73.2
Immature linyphiids	50.2	18.5	61.1	49.9
Other immatures	--	--	100	0

In contrast to grass, efficiencies of samplers for adult spiders in wheat were more comparable. Some differences were apparent in that the D-vac was relatively poor at sampling *Erigone* species compared to the G-vac (14.3% and 53.3% respectively for *E. atra*). Another epigeic species, *O. fuscus*, was sampled with a higher efficiency by both samplers (70% and 88.9% respectively). Epiphytic species were sampled with relatively higher efficiencies using the D-vac (73.2% for *T. tenuis* and 68% for *B. gracilis*) although no particular bias was evident for the G-vac sampler. A 100% recovery rate was observed for lycosids using both samplers. Densities though were low with only 6 individuals being present in the samples in total.

Immature linyphiids as a category varied widely in size and were sampled less efficiently by the D-vac than the G-vac in grass (18.5% and 50.2% respectively) although similar efficiencies for both the D-vac and G-vac were observed in wheat (49.9% and 61.1% respectively).

The regression in Figure 2-6 illustrates the high degree of equivalence for both samplers for the species in the 10 second samples in wheat (R-sq = 0.8565) Those points lying furthest from the regression line represent *B. gracilis* for which the D-vac had a higher sampling efficiency than the G-vac (68% and 42 1% respectively) and *E atra* which was more efficiently sampled by the G-vac (53 3% to 14.3% respectively) (Table 2-4) A regression was not possible for species in 10 second samples in grass owing to the very low numbers of adult spiders in the D-vac sample.

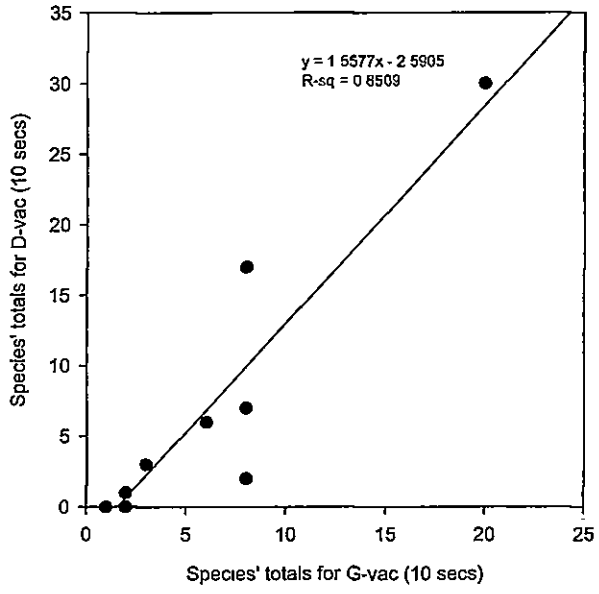

Figure 2-6 Regression between total number of each species sampled in 10 secs by G-vac and D-vac in wheat

2.5 Discussion

Sampling efficiency of the G-vac, particular for spiders in the largest size class, was greater than that of the D-vac in both wheat and grass. In wheat, although efficiency of the G-vac was greater, samples of small, medium and large spiders for both devices were proportionally similar to those of absolute values. In contrast, sampling from grass appears to present a greater challenge, with proportional differences to absolute values being observed for both samplers. Compared to the relative performance of the samplers in wheat, the D-vac's efficiency in grass was also substantially lower than that of the G-vac's. Differences in suction power and vegetation structure are the probable causes of this disparity.

For wheat alone, increased crop height was related positively to increased efficiency in sampling small and large size classes. This is surprising in that the greater drag caused by the taller vegetation may be thought to lower air speed and as a result reduce sampling efficiency. A possible explanation is that with increased cover, spiders tend to utilize the larger crop area thereby increasing their likelihood of being sampled. Other factors could be warmer temperatures increasing activity, and the relatively lower efficiency caused by the presence of chaff on the ground after harvest, when the crop was reduced to the height of stubble.

Although no similar positive relationships were observed in grass, the increased efficiency of sampling immatures in April, when the grass was at its tallest (29 cm), may also be indicative of a more diffuse distribution throughout the vegetation. This could result from higher densities of immatures in April and subsequent avoidance of predation, cannibalism and the related desire to disperse.

Irrespective of grass height, sampling efficiency of the D-vac reduced considerably for larger bodied spiders resulting in adults being substantially underestimated A possible cause is that grass constitutes a far denser matrix of vegetation, which in contrast to wheat is a physical characteristic that is relatively unaltered over time The lower suction power of the D-vac means that the air flow may not penetrate and dislodge spiders inhabiting the lowest and densest stratum of the grass Both the smaller size and greater vertical distribution of immatures may increase their sampling efficiency relative to adult spiders which as well as being heavier may tend to reside nearer the soil surface and thus further from the strongest air flow. The complement of species may also contribute to the lower efficiency in that a greater proportion of epigeal species occurring in grass may subsequently mean that fewer spiders are exposed to the strongest suction in the upper layer of the vegetation.

A study by Wright and Stewart (1992) used 15 repetitive samples in 3 grassland sites to compare the efficacy of D-vac and G-vac samplers Although the methodology is different to that used here, a comparison in terms of average ratios of D-vac to G-vac catches gives similar results for immature linyphiiids (Wright and Stewart 0 58 to this study 0 39) but not for adult linyphiids which were far higher in the other study (Wright and Stewart 0 36 to this study 0.05). The Wright and Stewart study gives no indication of when samples were taken, but it is unlikely that the results of this study are down-weighted by samples being taken over a longer period Efficiency may have varied owing to changes in the distribution of spiders in response to temperature or density, but as so few adults were collected and no peak in efficiency was observed, this does not seem plausible. The alternative explanation is that the suction power of the D-vac may have been lower in this study. Further evidence for this comes from the data for Chapters 5 and 6 where adult spiders were collected in appreciable numbers as well as

epigeal species not sampled here. A catastrophic failure of the D-vac used in previous studies necessitated its replacement by the sampler used in this study. Although the engine capacities were the same, the greater age, differing design and service history may have led to a difference in performance between these two devices.

Although the proportion of the size classes in the 10 second G-vac samples were significantly different to absolute values, the greater efficiency of the G-vac demonstrates that it is more suitable than the D-vac for sampling in grass. In wheat however, the limitations of nozzle diameter and length mean that the G-vac cannot be placed over the mature crop to sample an area similar to that of the D-vac's in one attempt. Removal of the greater portion of the wheat above the ground is not a practical proposition for most studies and therefore many more repeat samples are required, taken between the tillers, for the same sample area. Samu *et al.* (1997) found that repeated sampling with a G-vac overestimated densities for the same sample area as a whole unit. In taking numerous small samples, a greater length of 'edge' was exposed to spiders outside the sampling boundary over which they could be sucked in, thereby inflating the actual densities present.

The G-vac is more efficient overall and substantially so in grass where use of a device with a relatively lower suction such as the D-vac should be avoided. Whereas a G-vac may enclose the sampled vegetation as a whole in a ley field, its use in this fashion is not consistent in mature wheat where only a sampler with a larger and longer nozzle can enclose the crop. This may improve sampling of epiphytic species such as *T. tenuis* and *B. gracilis* and reduce over-estimation of densities by taking numerous small samples. Although the D-vac's ability to sample a larger area makes this device potentially useful in tall and robust crops, substantial improvements in the design with regards to weight

and suction power would need to be addressed to make these large sampling devices a viable alternative once more Overall, where one sampling device is to be applied, the G-vac is a better choice for these two crop types

Chapter 3. A novel trap to capture ballooning spiders

3.1 Introduction

Aerial dispersal by ballooning is a key strategy in the life histories of many spiders, especially pioneers of disturbed, patchy habitats exemplified by linyphiids in agricultural landscapes (Thomas, Blackshaw *et al.* 2003). Quantifying the dispersal power of these species is a necessary prerequisite for accurately modeling spatial population dynamics and developing successful sustainable management strategies. Various techniques that actively or passively intercept airborne spiders have been used to measure aspects of aerial dispersal. For example: the use of nets and sticky traps to measure aerial density at one or more altitudes (Greenstone 1991; Greenstone, Morgan *et al.* 1987; Thomas and Brain 2003) manual collection from fences, wire or string to quantify numbers passing a point or line per unit time (Thomas and Brain 2003; Vugts and Van Wingerden 1976); or water traps to quantify deposition rates per unit area (Thomas and Jepson 1999; Weyman, Jepson *et al.* 1995). These methods are either labor intensive, require operator attendance, cannot easily sample several locations at the same time, or may be cumbersome or expensive.

An alternative sampling method exploits the climbing behavior normally exhibited by spiders as a precursor to ballooning (Blackwall 1827); spiders climb to a high point where a silk line can be produced above the surrounding vegetation and where suitable atmospheric conditions for successful ballooning are likely to occur (Suter 1999). Sticks, canes or similar objects inserted into the ground, provide artificial platforms that stand higher than the surrounding vegetation. Spiders climbing and attempting to balloon from these can be observed, or caught and counted, to give a relative indication

of ballooning activity over a given period. Thorbek and Topping *et al* (2002) in a validation of this technique found that numbers of spiders observed climbing a 30 cm stick correlated well with numbers obtained from an aerial suction trap Using a similar technique to sample several habitats over time, Duffey (1956) applied a tacky adhesive to the tops of canes to trap climbing spiders However, the adhesive was adversely affected by hot, cold or wet weather and became clogged with winged insects during summer months

In this study a novel design is evaluated where the climbing-stick trap is developed to allow continuous unattended sampling without the use of adhesive. Attached to the top of a climbing-stick is a 'bottle-trap' operating on the lobster-pot principle Climbing spiders are retained within the bottle-trap until it is removed or replaced In this chapter the trapping efficiencies of climbing-sticks either with bottle-traps or with adhesive are compared

The trap collects spiders climbing from the underlying vegetation before they first become airborne, and spiders already airborne arriving at the trap from sources upwind No differentiation is made between these two potential sources. However the effect of suspending a net skirt from the climbing-stick to increase the effective vertical and horizontal cross-sectional area of the trap is evaluated. This increases both the source area of spiders emerging from the ground and the interception of airborne spiders.

3.2 Materials and methods

3.2.1 Trap development

Changes were made in the design and materials used in the construction of the trap after a period of field testing. The use of wooden dowelling as a naturally textured material for the climbing-stick proved to be unsuccessful, damage from wind and livestock occurring even after the diameter was increased from 5 to 8 mm. Use of aluminum climbing-sticks reduced instances of damage and the increased rigidity also assisted in the replacement of traps when ground conditions were very hard.

The attachment between the climbing-stick and bottle-trap was initially made using a cylindrical high-density foam insert, glued to the underside of the top section of the trap, the climbing-stick being pushed tightly into a hole in the insert, to provide the attachment. Deterioration of the foam through wind buffeting and high wind speeds caused bottle-traps to frequently be lost in inclement weather. An improved screw-in design was developed which significantly reduced these losses.

3.2.2 Trap construction

The 'lobster-pot' part comprising the bottle-trap was constructed from a standard straight-sided, clear plastic, 2-litre soft-drink bottle (Figure 3-1a). The body of the trap was made by first removing, with a heated scalpel blade, the material between the five reinforcing moldings in the base (Figure 3-1b). The top section of the bottle was then removed, just below the shoulder, approximately 9 cm from the top of the bottle opening (Figure 3-1c). A band approximately 7 cm deep was cut away from the main body and discarded. The removed top section was then inverted and fixed into the

remaining base section of the bottle using adhesive tape (Figure 3-1d), ensuring no gaps remained between the two sections. A 2 ml micro-tube screw-cap (Sarstedt™, A.G. Sarstedt and Co, Numbrecht, Germany) was glued with super-glue (Loctite™, Henkel, Düsseldorf, Germany) centrally beneath the now inverted base section and above the original bottle top opening forming the new base (Figure 3-1e) A 20 x 20 cm square of white voile gauze fabric was then fastened tightly over the five cut away openings with a rubber band (Figure 3-1f) The cut-away openings covered in fine gauze voile material allowed vertical air flow, general ventilation and, when removed, the extraction of spiders from the trap

The climbing-stick, made from a 1 5 m length of 7.9 mm diameter aluminum rod, was roughened with sandpaper to assist climbing spiders

An attachment for the bottle-trap was made using the body of the same 2 ml micro-tube from which the cap had been glued to the bottle-trap. The bottom section of the main body was removed just above the taper (Figure 3-2a). A small amount of rapid drying epoxy resin (Araldite™, Huntsman Advanced Materials, Everberg, Belgium) was applied to the inside of the tube, which was then place over the end of the climbing-stick with the thread end uppermost and extending approximately 5 mm above the end (Figure 3-2b).

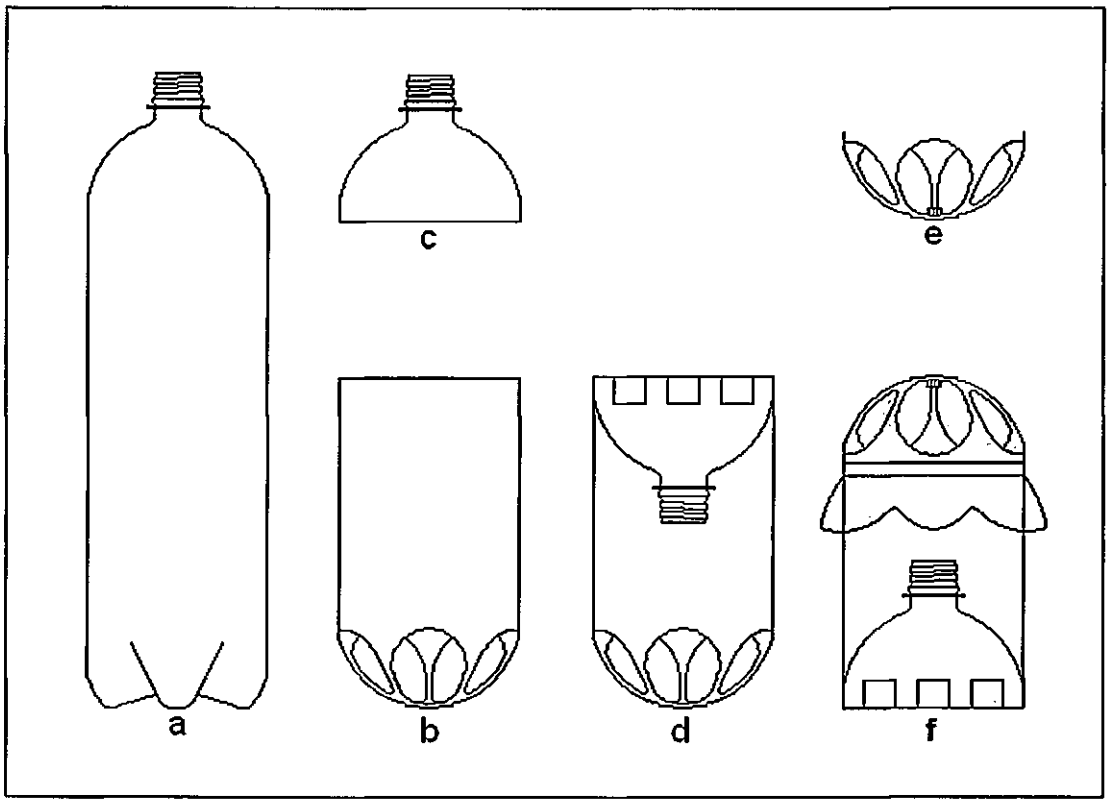

Figure 3-1. a, 2 lt plastic soft drinks bottle; b, bottle bottom with the five reinforcements removed; c, top removed and section below discarded; d, inverted top inserted into the remaining section and secured with adhesive tape; e, screw cap glued underneath the central hub; f, the finished trap with fine gauze fastened in place with a rubber band.

The net was constructed from 2 cm mesh bird netting made from a natural-fibre twine. Sufficient material to form a small tent was draped over a 1.2 m wooden pole. A 3.14 m length of 2 mm fencing wire, formed into a 1 m diameter circle (Figure 3-2c) was placed over the netting and pole to weigh down the base of the net and keep it splayed out. The netting was pulled taut over the pole, arranged evenly around the frame, and its hem secured to the circular base with wire ties before cutting away excess material. (Figure 3-2d).

3.2.3 Setting and operating the trap

To set the trap the climbing-stick was pushed vertically into the ground and a bottle-trap placed over and screwed to the top of the stick. If a net was also used, this was first pulled up to form a cone and the climbing-stick placed through the apex before the stick was pushed into the ground. The net was then clipped to the stick using a small bulldog clip set at an angle to ensure the spiders continued climbing The circular wire base was held down with wire pegs or stones. The bottle-trap was then screwed to the top of the stick (Figure 2e).

For continual sampling bottle-traps were unscrewed and replaced with empty ones For daily samples reported here, traps were typically changed each evening after ballooning behavior had finished. Removed traps were placed in plastic bags in the field before returning to the lab Spiders were extracted from traps by removing the voile gauze and shaking vigorously over a tray from which spiders were collected with an aspirator Any spiders remaining in the trap were either aspirated or, if there was a lot of silk in the trap, removed with a small paint brush.

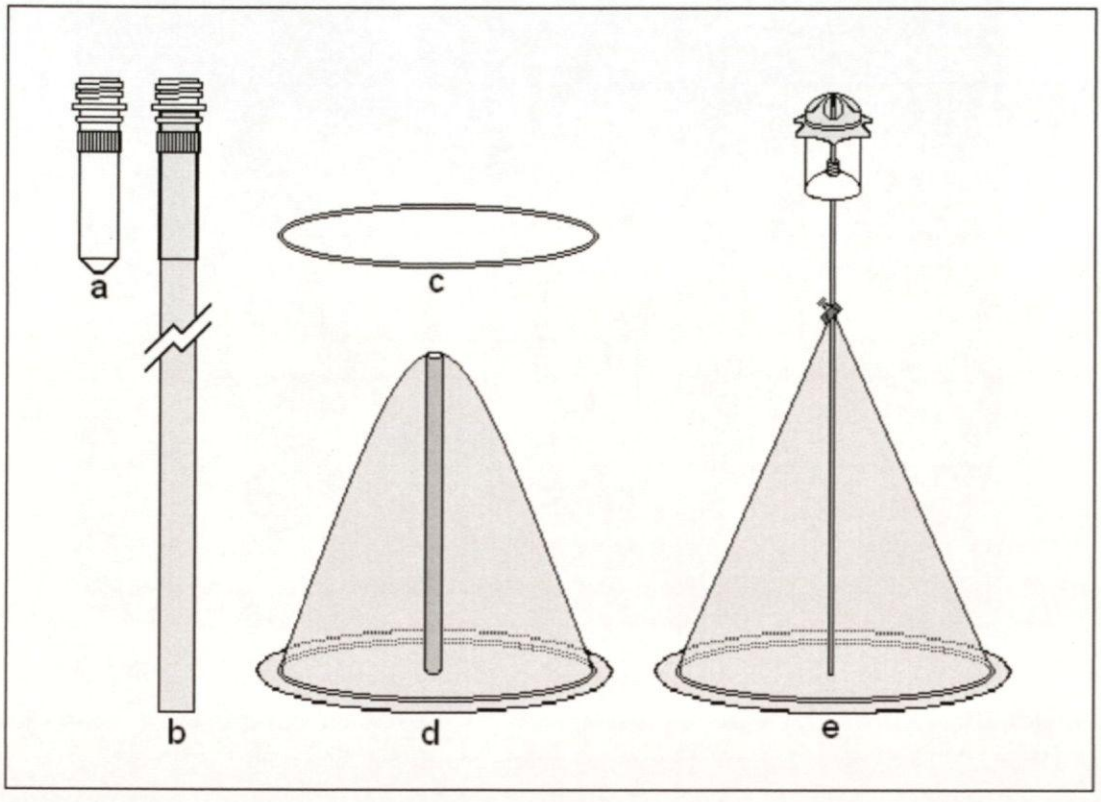

Figure 3-2. a, Micro-tube; b, micro-tube with bottom removed pushed over the end of the climbing-stick and glued in position; c, circular wire frame; d, netting pulled over pole with circular wire frame placed over netting; e, finished trap with bottle-trap screwed on and net clipped to stick.

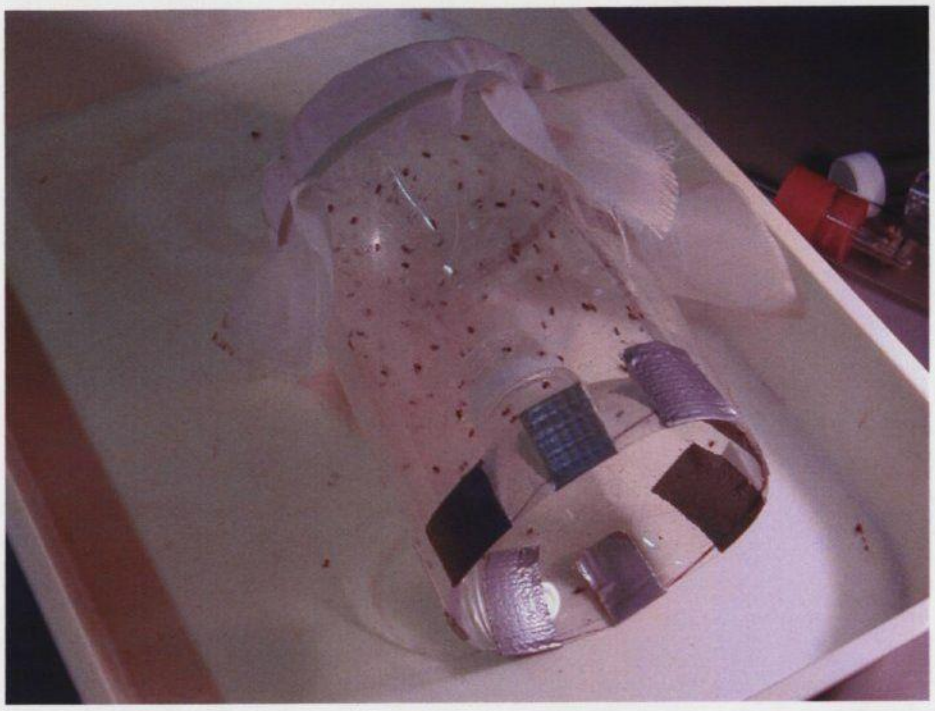

Figure 3-3. Side view of trap prior to emptying spiders into the tray for sorting.

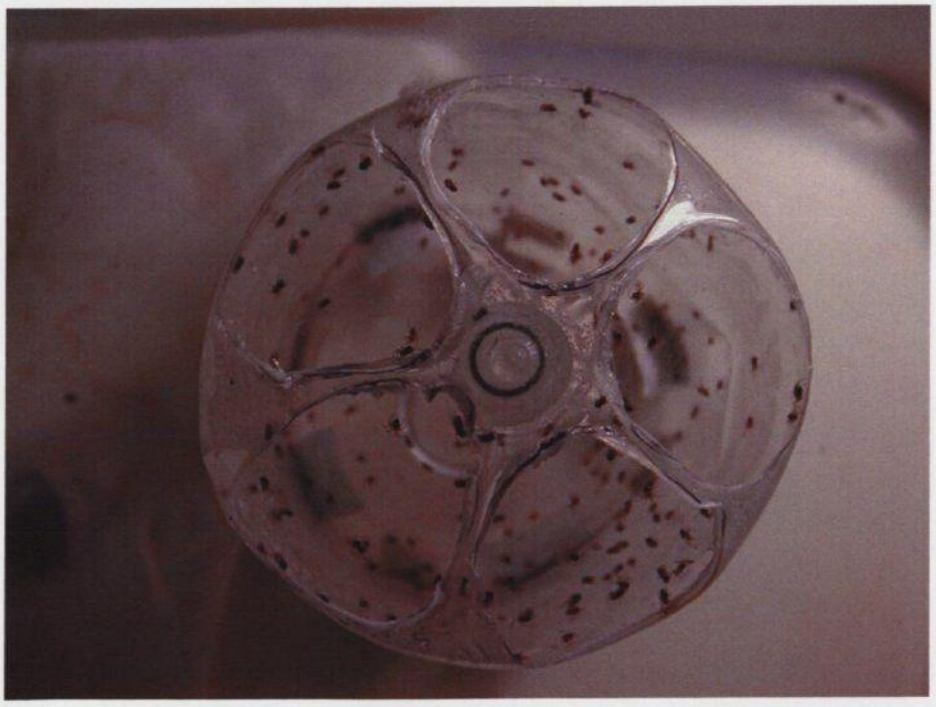

Figure 3-4. Top-view of trap with voile removed, showing a day's catch of spiders.

3.2.4 Trap evaluation

Experiments were performed with traps set along a transect in an 8 ha grass field on the the Seale-Hayne Faculty estate farm, Newton Abbot, Devon, in the southwest of the UK. The temporary grass ley was approximately 150 mm tall at the time of sampling. The transect of traps was surrounded by an electric fence to prevent disturbance by sheep and cattle that periodically grazed the field.

Three aspects of the trap were evaluated: catch size from climbing-sticks with bottle-traps compared with climbing-sticks with a polybutene-based insect trapping adhesive (Oecotak A5™, Oecos Ltd, Kimpton, Hertfordshire, England) applied to the uppermost 15 cm of the stick.; catch size from climbing-sticks and bottle-traps with and without nets; and retention of spiders left in bottle-traps during the day and overnight.

Catch size from climbing-sticks with either bottle-traps or adhesive was compared by placing 10 traps of each design in a single line transect. Traps of each type were set alternately along the line at 10 m intervals. Bottle-traps were emptied on each of 11 successive days in March 2003; climbing-sticks with adhesive accumulated spiders over the same period. Climbing-sticks with adhesive were checked periodically to ensure that the accumulation of trapped spiders or insects was not excessive and that there was ample exposed adhesive to maintain capture efficiency. Total numbers caught per trap were recorded at the end of the sampling period. For catch size evaluations comparing climbing-sticks and bottle-traps with and without nets, samples were taken daily over a 13 day period in March 2004. For the retention study 10 climbing-sticks with bottle-traps were placed in the field as above. Numbers of spiders in each bottle-trap were recorded after 24 h at 17:00. Traps were then relocated to a tarmac substrate away from

ground vegetation to minimize further ingress of spiders. Numbers of spiders remaining in the traps were again recorded at 09:00 and at 17:00 the following day.

Comparisons of trap type and bottle-traps with and without nets were analysed using oneway ANOVA with data being transformed by log(n+1) to stabilise the variance.

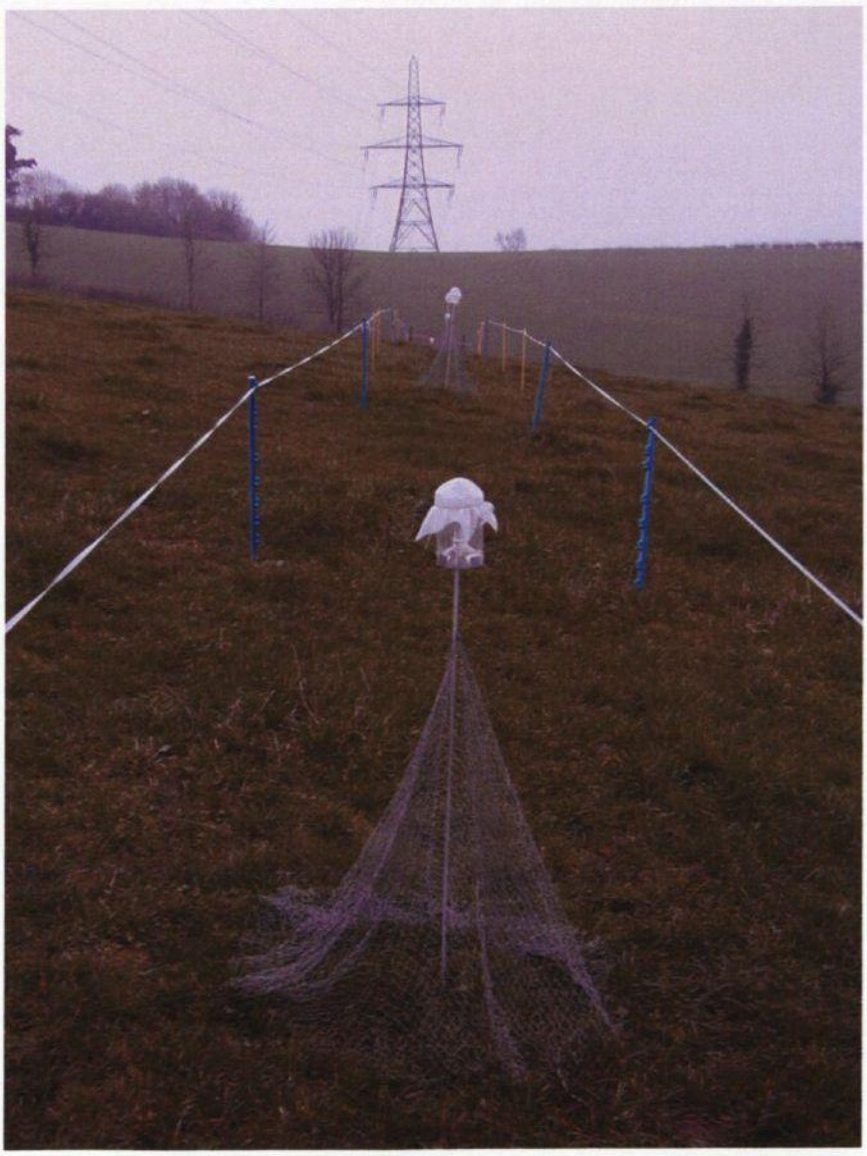

Figure 3-5. Transect of traps with nets in grass ley, protected by electric fence.

3.3 Results

3.3.1 Comparison between climbing-sticks with bottle-traps and climbing-sticks with adhesive

Catch sizes were significantly higher in bottle-traps compared with climbing-sticks with adhesive ($F_{(1,18)} = 30.11, P < .0001$) (Table 3-1). Average catch size (± SE) for climbing-sticks with bottle-traps was 56.4 ± 12.853 and for climbing-sticks with adhesive 6.6 ± 1.4. Total catch size over the period for climbing-sticks with bottle-traps was 564 spiders and for climbing-sticks with adhesive, 66 spiders.

Table 3-1. Total number of spiders caught per trap over an 11 day period from climbing-sticks with bottle-traps and climbing-sticks with adhesive.

Trap N°	N° per trap over 11 day period	
	Bottle-trap	Adhesive
1	18	1
2	17	6
3	14	8
4	46	9
5	78	6
6	107	5
7	131	16
8	75	7
9	53	8
10	25	0

3.3.2 Comparison between bottle-traps with and without nets

Spiders were not recorded in any trap on 22, 23, 24, 28, and 29 March when high wind speeds suppressed ballooning activity (Figure 3-6). Traps with nets caught significantly more spiders than those without nets on 18, 19, 20, 21, 25 and 30 March (Table 3-2). No significant difference was recorded on 26 March though catch size was particularly low for this day. Total numbers of spiders caught by traps with and without nets were

641 and 218 respectively. Over the 13 day period numbers caught in traps with and without nets were positively correlated (R-sq = 0 985, P < 0 0001).

Table 3-2. Daily totals of spiders caught for all traps with and without nets

Date	Daily N° in traps		F-ratio	Significance
	Nets	No Nets	(DF 1,18)	
18/3	14	2	5 62	**
19/3	324	137	10 69	**
20/3	41	8	11 55	**
21/3	46	7	17 38	**
22/3	0	0	-	-
23/3	0	0	-	-
24/3	0	0	-	-
25/3	147	57	7 02	*
26/3	4	1	1 46	NS
27/3	1	1	-	-
28/3	0	0	-	-
29/3	0	0	-	-
30/3	64	5	26 16	***
* = p < 0 05, ** = p < 0 01, *** = p < 0 001, NS = not significant				

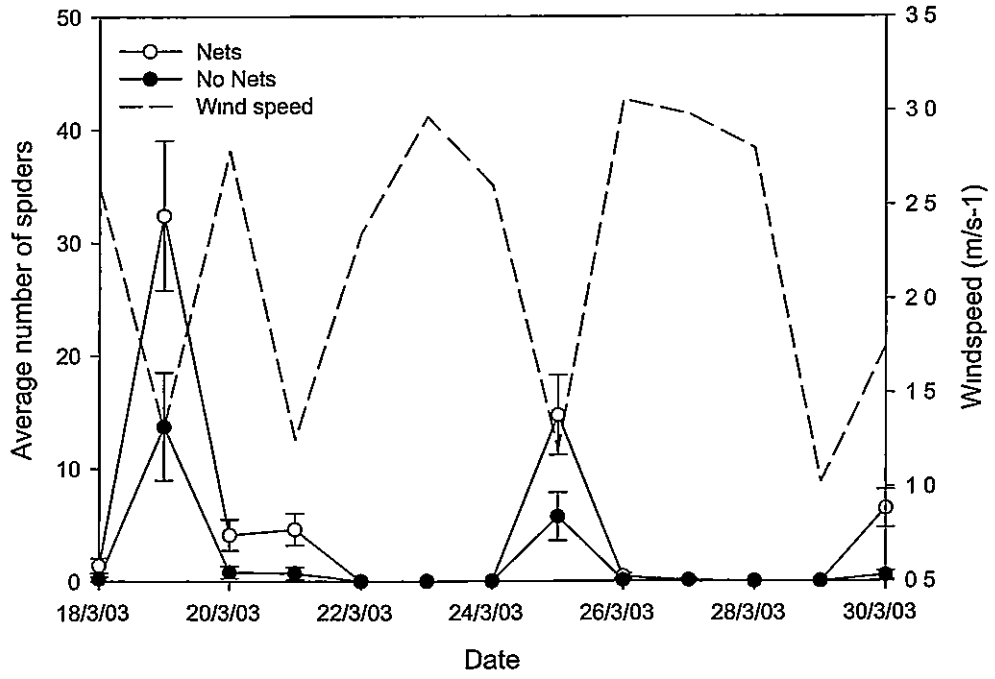

Figure 3-6 Average numbers of spiders trapped by climbing-sticks with and without nets with recorded wind speed

3.3.3 Retention of spiders in bottle-traps

Of a total of 413 spiders in 10 bottle-traps recorded at 17:00, 69 (15.3% ± 11.8%) had escaped by 09:00 the following morning. A further 35 (9.1% ± 7.7%) escaped between 09:00 and 17:00. The average loss over 24 h was 24.4% ± 16.6%. A significant linear regression (R-sq = 63.6%, P = 0.004) between initial numbers caught and numbers lost after 24 h indicated losses to be density independent (Figure 3-7). Mean rate of loss (± SE) from traps between 17:00 and 09:00 was 0.431 ± 0.141 spiders per hour and from 09:00 to 17:00, 0.438 ± 0.148 spiders per hour. No significant difference in rate of loss was observed between night and day hours ($F_{(1,18)} = 0.01$, P = 0.976).

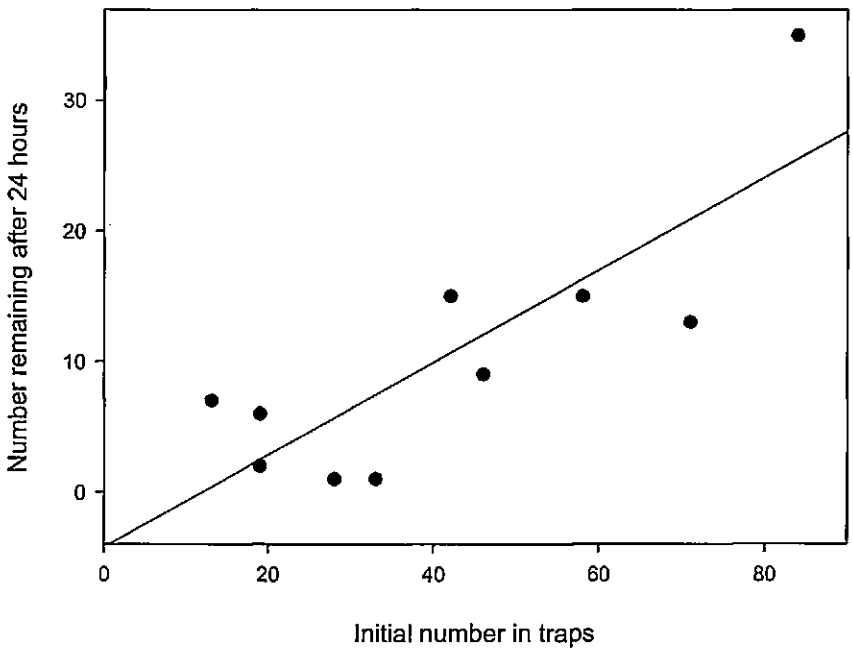

Figure 3-7. Regression plot of initial number in traps against number remaining after 24hours (loss = -4.210 + 0.3538 Initial number).

3.4 Discussion

Climbing-sticks with bottle-traps ('stick and bottle' traps) are extremely effective, cheap and easy to make and use The cost of construction materials is estimated to be less than £7 per trap at current prices. Apart from the greater catch size, which, in total, was over eight times that of climbing-sticks with adhesive, the bottle-traps also retain the advantage of easy replication and the ability to simultaneous sample different habitats at large spatial and/or short temporal scales The retention of live spiders means trapping agents such as adhesive or water and detergent are not required Furthermore, additional behavioral, ecological or genetic studies can be carried out on the trapped spiders if required

The addition of nets to climbing-sticks with bottle traps increased catch size almost three fold The positive correlation observed between numbers caught in traps with nets and those without implies that increased ballooning activity during periods of low wind speed resulted in greater catch sizes in both cases Nets present a larger 'footprint' on the surface compared to climbing-sticks which may increase collection of spiders from the area directly beneath the traps at the start of ballooning activity. However it is likely that, during the course of a prolonged ballooning event, the catch of spider will increasingly represent spiders originating from outside the local vicinity of the traps which have been intercepted by the nets whilst airborne.

The trials reported here were conducted in short grass In other trials conducted in taller crops such as wheat, it was necessary to use 2 5 m climbing-sticks to raise the nets and bottle-traps above the crop in order to intercept airborne spiders. For comparative work

sampling airborne spiders above crops of differing height, traps should be set at a constant height above the roughness length of the vegetation.

Although losses from traps left operating for several consecutive days can be estimated, it is recommended that the traps are emptied daily, unless spiders are being collected only for laboratory studies. This avoids large amounts of silk accumulating inside the bottle-traps which makes separation of the spiders from the silk difficult and extraction much more time-consuming. Similarly, when large numbers of spiders were caught within a single day, it was found that traps were best emptied immediately after collection because of the quantity of silk produced if left overnight. Traps were best removed in the evening after ballooning had finished. If traps cannot be changed until the morning, it should be carried out very early during summer months, in order to prevent cross contamination with the previous day's sample. If longer duration sampling is required and live spiders are not, a preserving fluid could be introduced into the bottom section of the bottle-trap. Spiders would fall into this, thereby reducing losses and minimising any build-up of silk.

A large variation in catch size was observed along the transect, particularly for the bottle-traps. A possible reasons for this is the greater interception efficiency of the bottle-traps coupled with the undulating nature of the field which exposed traps along the transect to different wind speeds depending on elevation. Greatest catch size was recorded at the highest elevation which owing to a long, unimpeded fetch length to the southwest, received a greater through-flow of air than other traps and hence greater numbers of spiders were intercepted.

Linyphiids were by far the commonest spiders caught by the traps, being highest both in numbers and in occurrence throughout the year. Other spiders caught in lesser numbers belonged to the families Thomisidae and Araneidae Though immature thomisids were observed ballooning, adults of these families may have been present in traps as an accident of other behaviours such as rigging, locating shelter/feeding sites or web building. Care must therefore be taken before attributing dispersal by ballooning to all spiders caught

The bottle-traps sometimes caught other insects including bush crickets, cantharid beetles, ephemeropterans, plecopterans, tipulids and various other dipterans. Some of this by-catch might prey on spiders but no evidence of this was observed Other potential losses are likely from predation among spiders but this was not quantified and is likely only if traps are left operating unchanged for longer periods.

An improved comparison of the effectiveness of the different trapping methods could have been achieved if trapped spiders had been recorded on the climbing-sticks with adhesive on a daily basis. This would have given a rate of accumulation which could have been compared directly with the daily catches from the climbing-sticks with bottle-traps.

These traps provide a relative estimation of ballooning activity over a given period Their use for providing estimations on either the numbers of spiders ballooning during a ballooning event, or the numbers of spiders landing in a certain area could be problematic. To estimate numbers of spiders ballooning (or density of airborne spiders) the volume of sampled air should be measured accurately This has been previously attempted using a spinning rotary trap (Topping, Sunderland *et al.* 1992). Although

ground populations of spiders could be isolated using a cover, preventing spiders from climbing from the area beneath the trap, the proximity of the bottom of the net to the ground surface and corresponding interaction between the ground and the air could make estimations of the volume of air sampled difficult to calculate. In respect to quantifying spiders arriving in a certain area, the catch of the traps represent both those spiders which may have been about to land and those that could have traveled further but were intercepted. Also many spiders make repeated ballooning flights (Thomas and Brain 2003) and therefore the presence of a spider in a particular location cannot be related meaningfully to the number of spiders that the area may receive after the end of the ballooning event. Calculation of the net difference in ground population density after a ballooning event has been attempted by comparing densities in cages excluding immigration to non-caged areas after a ballooning event (Topping and Sunderland 1994). The accuracy of the estimation was limited by the patchy distribution of spiders in the field.

Chapter 4. Dispersal of spiders on farmland in the southwest, UK

4.1 Introduction

Previous studies have been undertaken where ballooning activity has been monitored over several months (Blandenier and Fürst 1997; Duffey 1956; Thomas and Jepson 1999). At present no study on ballooning activity in spiders has been performed in the southwest of the United Kingdom which comprises a greater proportion of mixed farms with grazing land compared to arable farmland in the southeast. This study partially replicates that of Weyman *et al.* (1995) which compared seasonal ballooning activity to changes in ground population density and ballooning tendency as measured in a wind chamber. The trapping method used here is the climbing-stick trap described in Chapter 3. This trap is highly effective at collecting large numbers of agrobiont spiders and therefore may accurately reflect ballooning activity over the landscape area.

The objectives of this study to were to determine if:-

i. agrobiont linyphiids placed in a wind chamber exhibited species-specific differences in their propensity to balloon
ii. ballooning propensities observed in the chamber varied on a seasonal basis
iii. agrobiont species exhibited species-specific ballooning activity in the field and if so whether ballooning frequencies related to changes in ground population density or differences in seasonal ballooning motivation observed in the laboratory

4.2 Behaviour of spiders in the wind chamber

4.2.1 Materials and methods

Seasonal motivation in ballooning was investigated independently of field sampling in 2005. A wind chamber was used to elicit pre-ballooning behaviour in spiders collected over the course of the year The wind chamber (Figure 4-1, Figure 4-2) constituted a box constructed from 4 mm clear acrylic sheeting, measuring 29 cm in height, 65 cm in width and 100 cm in length through which an air flow was generated by two tangential (cross-flow) fans, mounted at one end (total fan length 60 cm, fan diameter 6 cm) This type of fan was chosen as the outflow of the air was even across the width of the fans' surface. Each fan was driven by an AC single-phase induction motor which allowed for a triac (triode for AC) based speed control A domestic lighting dimmer switch was adequate for this purpose enabling a wide degree of speed control down to very low fan speeds, the resistance rating being high enough for the inductive loading of the motor. The fans outflow across the sticks (see below) produced a light, turbulent wind current throughout the chamber. A hot-wire anemometer recorded wind speeds 15 cm from the fan fluctuating between 0.10-0.46 m/s, and 15 cm from outflow end, between 0.09-0 42 m/s Wind speeds also fluctuated between the top and bottom of the sticks with no clear differentiation in strength

On the floor of the wind chamber, a layer of 'egg-box' foam was fitted, into which sticks, 16 cm and 5 cm in length, were placed alternately at the top of each prominence This created a lattice arrangement with a distance between each stick of 3 cm. The regular undulating surface allowed spiders on the ground to locate a stick at any point by following the surface inclines The only exception to this was the sides of the chamber where no sticks were present. Some spiders on reaching the edge of the foam

had a tendency to follow the wall of the chamber. Spiders remaining at the wall for more than 20 seconds were lifted gently using a fine paint brush, and moved back to the ground adjacent to the starting position (stick). The foam was raised slightly at the outflow end to preserve the direction of airflow over the back wall.

Spiders to be tested in the chamber were collected each month from the nearby fields using a G-vac sampler. Species were identified and placed separately into clear plastic pots 46 mm in height and 90 mm in diameter. The bottom of each pot contained a 10 mm layer of moist Plaster of Paris to ensure a constant high humidity to prevent spiders from dehydrating. Pots were kept outside in a shaded area and brought into the laboratory for testing which occurred within two days of collection.

All spiders were released onto the upper portion of the same stick situated near the mid line of the chamber approximately 20 cm from the outflow end. The behaviours recorded are described in Table 4-1. Duration of behaviours were recorded over a 3 minute period using the Etholog behavioural transcription program (Ottoni 1999).

Figure 4-1. Wind chamber showing tangential fans and dimmer speed control. The intakes of the fans are reversed (one up, one down) to allow the fans to abut. The motors being on the same side prevented this arrangement when the intakes were in the same direction.

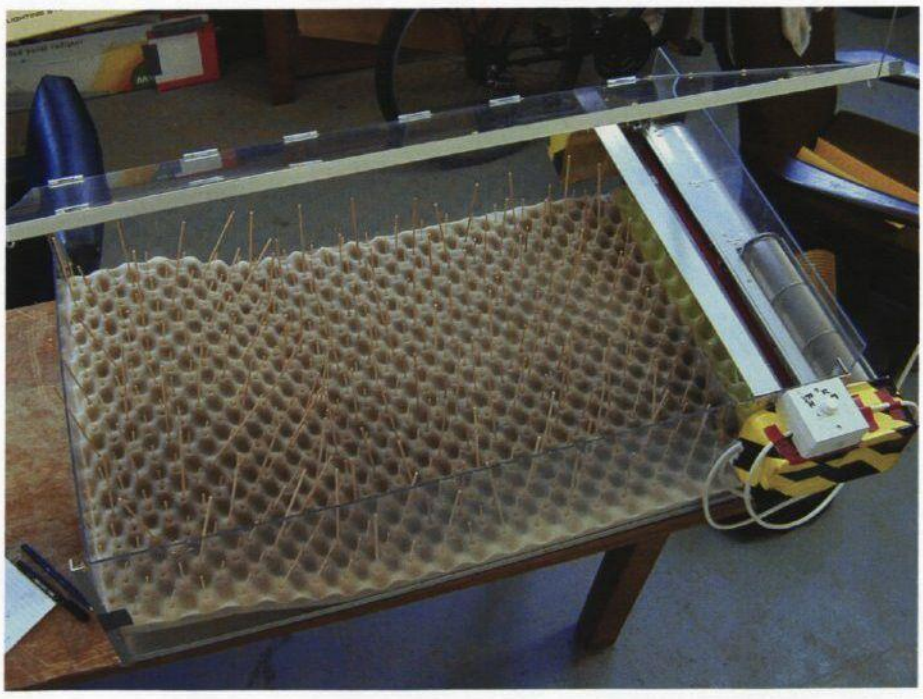

Figure 4-2. Wind chamber showing surface of 'egg-box' foam with wooden sticks positioned at the top of each prominence.

Table 4-1. Definitions of behaviours of spiders recorded in the wind chamber.

Behaviour		Description
Tiptoe	—	Pre-ballooning behaviour - spider faces into the wind, raises the abdomen and rears up on the ends of the tarsi in a 'tiptoe' stance (Figure 4-3). A precursor to the release of ballooning silk into the air, although rapid shifts to dropping, hauling, rigging and climbing may occur between attempts. Occurs on a horizontal or vertical surface but usually above the ground.
Drop	—	Pre-ballooning behaviour - spider drops on a length of silk facing into the wind with legs gathered but with a single hind leg extended straight. This action may be to either increase the long axis of the spider to help it maintain position whilst suspended, or to facilitate the release of ballooning silk possibly to ensure its separation from the dragline. Alternatively the extended leg may provide sensory information from the trichobothria on wind speed/direction.
No tiptoe /drop	—	Pre-ballooning behaviour - release of silk when not in the above positions. Occurs occasionally during rigging. May be synonymous with 'rafting' (Bell, Bohan *et al.* 2005)
Balloon	—	Spider becomes airbourne after releasing silk into the air.
Rig	—	Spider traverses silk released by the spider (or other spiders) which is caught between sticks above the ground.
Haul	—	Silk released by the spider (or other spiders) is attached at the stick but not under tension. This is 'hauled in' and gathered by the forelegs whilst the spider is above the ground. May occur either on a stick or whilst rigging. Silk is discarded. The purpose may be either to clear silk which may impede further attempts at ballooning or to gather in slack from a released line which may be traversed if tension indicates the silk has caught further downwind.
Climb	—	Spider climbs vertically up or down sticks. This may be accompanied by a 'waving' action of the forelegs possibly in an effort to locate silk lines on which to rig.
Lower	—	Spider lowers on a dragline but does not assume the 'drop' posture and continues to the ground surface.
Ground	—	Spider is active on the ground surface.
Inactive	—	Spider is inactive either above or on the ground.
Groom	—	Spider is usually stationary and displays grooming behaviour such as drawing palps or tarsi through the chelicerae.

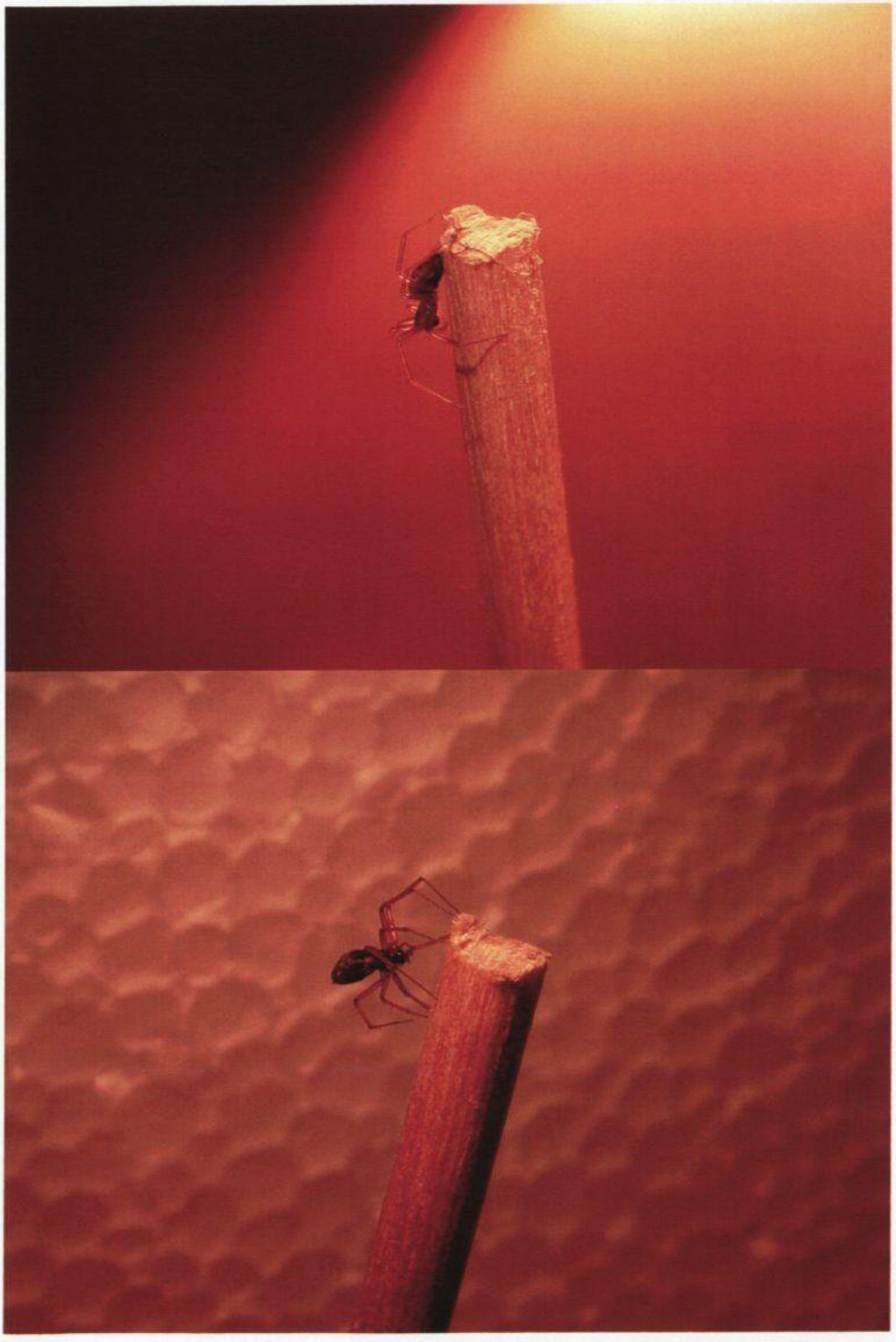

Figure 4-3. *T. tenuis* female in normal posture above and in 'tiptoe' posture below.

4.2.2 Results

A range of species were collected each month by suction sampling, however only *E. atra* and *O. fuscus* were collected in sufficient quantities to provide an adequate comparison over a range of months.

4.2.2.1 Behaviours expressed in Erigone atra and Oedothorax fucsus

From the proportion of time spent in each behavioural state, it is clear that *E. atra* (Figure 4-4) and *O. fuscus* (Figure 4-5) have a distinctly different response to the wind chamber environment. Although climbing in each species accounted for a fifth to a quarter of the total time spent in the chamber, 'tip-toe' and 'drop' behaviours were virtually absent in *O. fuscus* yet made up almost a third of all activity in *E. atra*.

'Inactive' was the most prevalent state in *O. fuscus*. Spiders which were active tended to move along the ground but also frequently climbed to the top of sticks before rapidly descending and moving to another. In this manner, some *O. fuscus* climbed numerous sticks in the 3 minute period. *E. atra* spent a far higher proportion of time above the ground engaged in behaviours associated with ballooning and traversing and manipulating silk.

Very similar results were observed for the males of each species. *E. dentipalpis* and *O. retusus* also showed the same distinct difference in ballooning tendency as displayed between *E. atra* and *O. fuscus*.

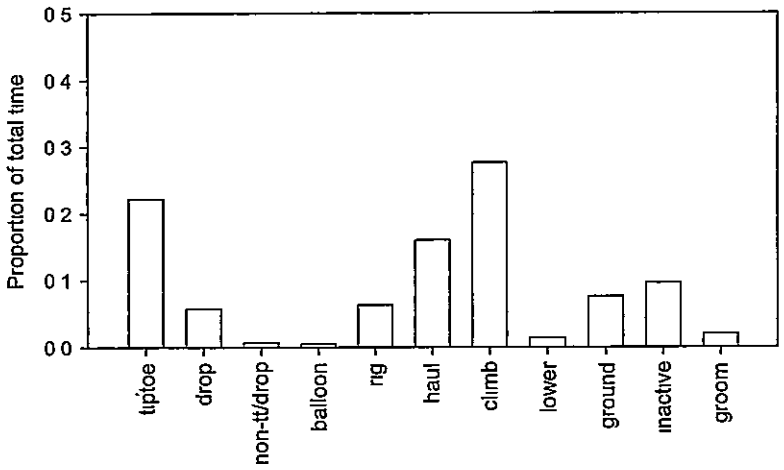

Figure 4-4 Proportion of time in behavioural states relative to total run time for 161 female *E atra* (3 minute run duration per spider)

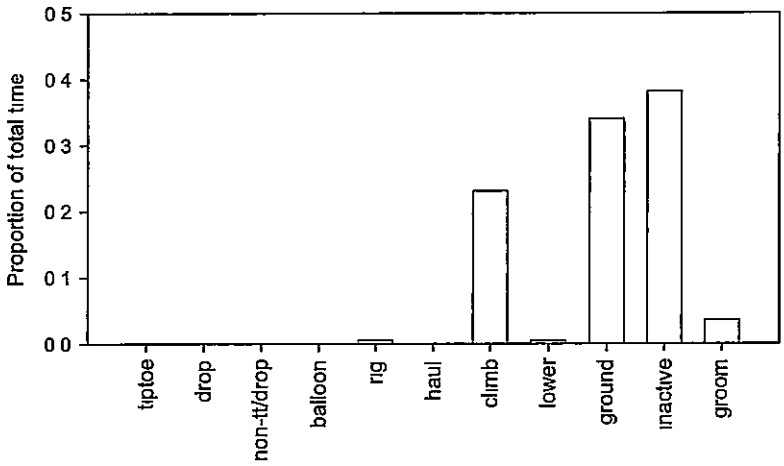

Figure 4-5 Proportion of time in behavioural states relative to total run time for 143 female *O fuscus* (3 minute run duration per spider)

4.2.2.2 *Pre-ballooning/ballooning behaviour and latency*

Pre-ballooning/ballooning behaviour and latency were only analysed for *E. atra*, these behaviours being rarely expressed in *O. fuscus* in the wind chamber. The total proportion of time in pre-ballooning/ballooning behaviour, and the time taken to exhibit pre-ballooning behaviour (latency) was calculated for a range of months.

Average time spent in pre-ballooning/ballooning behaviour was higher for specimens collected in July, September and October than in earlier months (Figure 4-6). A one-way ANOVA (Welch F test for unequal variance) was performed on the time spent in pre-ballooning/ballooning behaviour each month by *E. atra* females. A significant difference was observed between months ($F = 4.406_{5.5,18}$, $P < 0.001$) and an *a posteriori* Tukey HSD test indicated significant differences between March and July ($Q = 4.966$, $P < 0.001$), March and September ($Q = 4.906$, $P < 0.001$), May and July ($Q = 4.616$, $P = 0.019$) and May and September ($Q = 4.556$, $P = 0.022$).

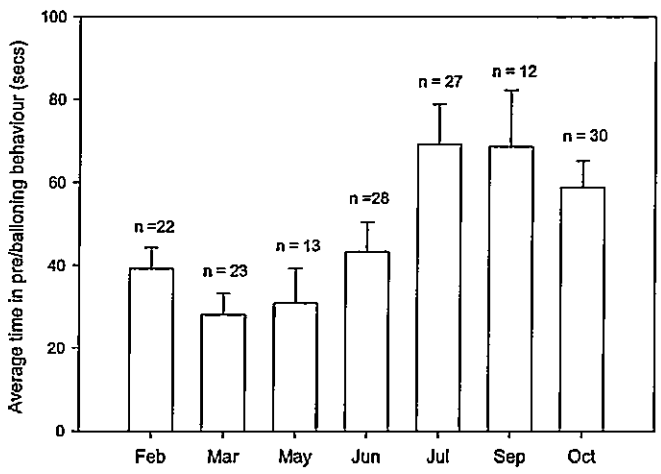

Figure 4-6. *Erigone atra* females. Average and SE of time spent in pre-ballooning/ballooning behaviour in a three minute period.

Latency of pre-ballooning behaviour was lower in July and October compared with earlier months (Figure 4-7) A one-way ANOVA (Welch F test for unequal variance) revealed significant differences between months for latency in *E. atra* females ($F = 4.425_{52\,62}$, $P < 0.001$) and a Tukey HSD test indicated a significant difference between May and October ($Q = 4.362$, $P = 0.033$)

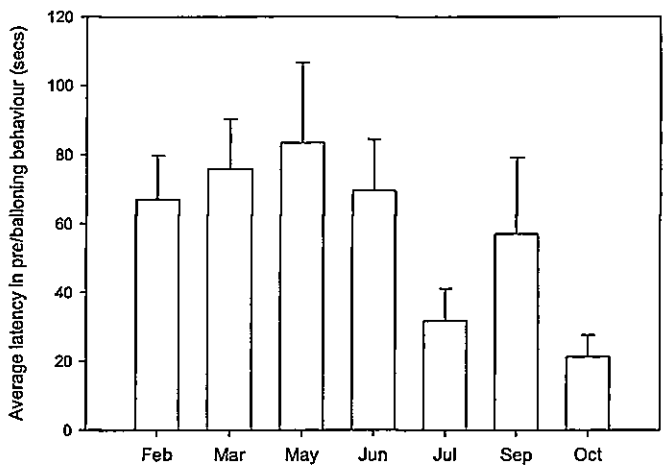

Figure 4-7 *Erigone atra* females Average and SE of latency before first expression of pre-ballooning behaviour

A one-way ANOVA revealed a significant difference in time spent in pre-ballooning/ballooning behaviour between months ($F = 2.576_{102}$, $P < 0.0422$) for *E atra* males (Figure 4-8) No significant differences were observed between individual months although September and October were close to significance ($Q = 3.902$, $P = 0.053$)

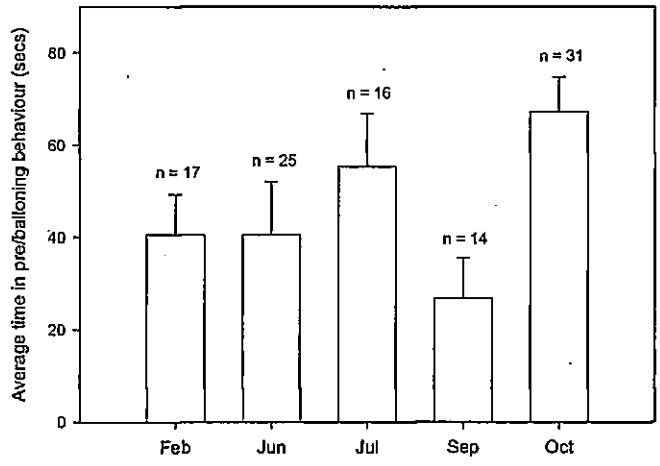

Figure 4-8. *Erigone atra* males. Average and SE of time spent in pre-ballooning behaviour in a three minute period.

Latency in *E. atra* males was lower in July and October (Figure 4-9) and a one-way ANOVA (Welch F test for unequal variance) between months was significant ($F = 3.292_{41.28}$, $P = 0.02$) although a Tukey HSD test did not indicate significant differences between individual months.

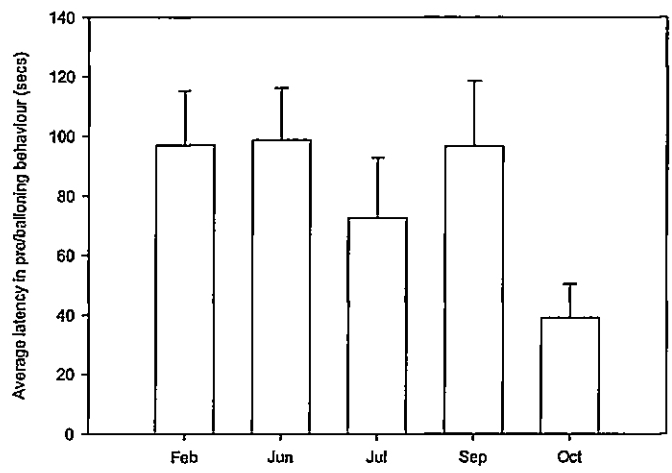

Figure 4-9. *Erigone atra* males. Average and SE of latency before first expression of pre-ballooning behaviour.

4.3 Dispersal of spiders in the field

4.3.1 Materials and methods

Ground populations and dispersing spiders were sampled from an 8 hectare, 2 year old temporary ley on the Seale-Hayne Faculty estate farm between September 2003 and February 2005 Dispersing spiders were sampled using the climbing-stick traps described in Chapter 5. Ten climbing-stick traps were set at 10 m intervals in a line transect running in a north-south direction. The transect was surrounded by an electric fence to prevent disturbance by livestock, the ungrazed area being managed by occasional grass trimming. Operations in the field included a silage harvest in May followed by periodic grazing by cows and sheep Grazing intensity was typically low with adjoining fields being accessible to livestock.

Climbing-stick traps were emptied daily during the week at approximately 18.00 with spiders being preserved in ethanol. Traps were kept open at weekends and for longer periods where daily collection was not possible For samples where spiders were taken over 2 or more days, numbers caught were divided by the number of days to give an average catch for that period. Ground populations were sampled monthly between February 2004 and November 2005 using the G-vac suction sampler (Flymo BVL-320) described in Chapter 2. A longer period of D-vac derived data from September 2004 until November 2005 was also obtained but owing to the lower efficiency is only referred to for periods outside the G-vac dates.

Owing to the large numbers of dispersing spiders caught, the results presented here represent a subset of the total days sampled One week of samples were selected per month in accordance with the timing of the ground population samples. As the sampling

period for dispersing spiders exceeded that of the ground population, the first week in the month of climbing-stick samples was selected for identification where a corresponding ground population sample wasn't available. The single week of sample collections per month when totalled over the 20 month sampling period consisted of 149 collections of the traps from the field. One hundred and thirteen of these collections represented single days, 32 two days (mostly weekends), 3 three days and 1 four day period. The total number of days sampled in the subset was 190 days.

All adult spiders were identified to species. Immature spiders were identified where possible to family with lycosid and thomisid immatures being distinctive. Immatures of other families such as theridiids and araneids were more problematic and were only distinguished when diagnostic features could easy be discerned, usually at the later developmental or sub-adult stage.

Wind speed data were collected using an A100R reed switch anemometer (Vector Instruments) connected to a DL2e data logger (Delta-T) at heights of 2 and 5 metres. The station was sited in the same field but at the edge and lower than the traps. Because of its lower position, the 2 m anemometer was considered to be somewhat sheltered and so only data from the 5 m anemometer was related to dispersal activity.

4.3.2 Results

Of the subset taken from the climbing-stick samples, a total of 22,704 spiders were collected in an 18 month period between September 2003 and February 2005. From G-vac samples a total of 2930 spiders were collected between February 2004 and November 2004. The aerial samples comprised 38 species of linyphiids and 24 species

of non-linyphiids from 9 families From the ground samples 19 species of linyphiids were identified and 5 species of non-linyphiids from 4 families. The most abundant aeronaut was *O. fuscus* (6732) followed by *E atra* (4502). The most frequent aeronaut was *E atra* being found in 111 of the 149 samples followed by *O. fuscus* (86) although immature linyphiids were as a group more frequent (88). The most abundant non-linyphiid in the traps was the theridiid *Robertus arundineti* (O -P -Cambridge) (450) followed by the tetragnathiid *Pachygnatha degeeri* Sundervall (351) *Robertus arundineti* was also the most frequent non-linyphiid aeronaut being found in 58 of the 149 samples and immature thomisiids, comprising mostly *Xysticus cristatus* (Clerck), were the second most frequent at 43, although there may be some doubt whether all thomisiids were intending to disperse Spiders were found in traps in 140 of the 149 samples which represented a maximum of 180 of the 190 days where aerial activity could have occurred Daily catches for samples containing 2 or more days were not determinable Of the samples representing single days, dispersal activity was recorded in 104 of the 112 days (see Appendix 1 for list of species and relative abundance of adults).

4.3.2.1 Effect of wind-speed on ballooning

Median wind speeds (Figure 4-10) relative to the subset of samples selected each month showed no obvious seasonality although differences between the 1st and 3rd quartiles tended to be smaller during the summer months. The mean wind speed over the whole period was 2.79 m/s. Low median wind speeds were recorded in the months of February, November and December, 2004

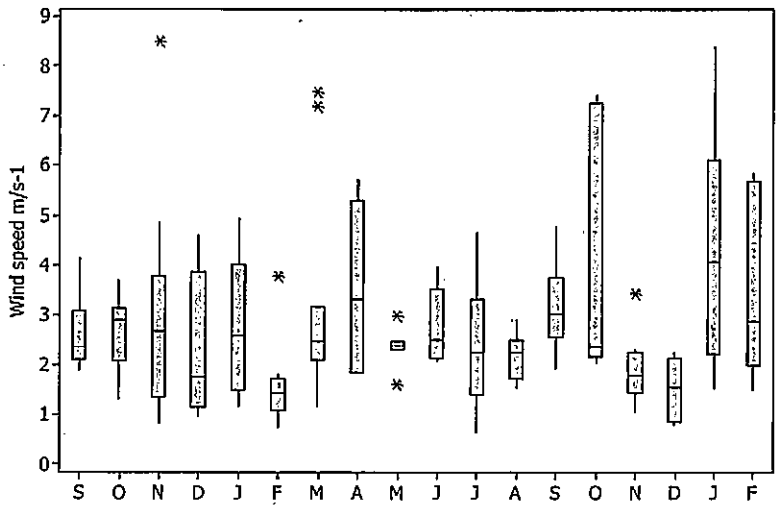

Figure 4-10. Median wind speeds for the subset of samples selected each month between September 2003 and February 2005. Asterisks indicate outliers.

Between wind-speeds of 2 to 2.5 m/s (Figure 4-11) the number of spiders dispersing is seen to become increasingly limited by the higher wind speeds which account for a progressive smaller increment of the cumulative catch. Using the median of the samples (2.356 m/s) as a reference, the average catch of spiders per sample day below the median was 293. Above the median wind-speed the average catch decreased to 20 spiders per day.

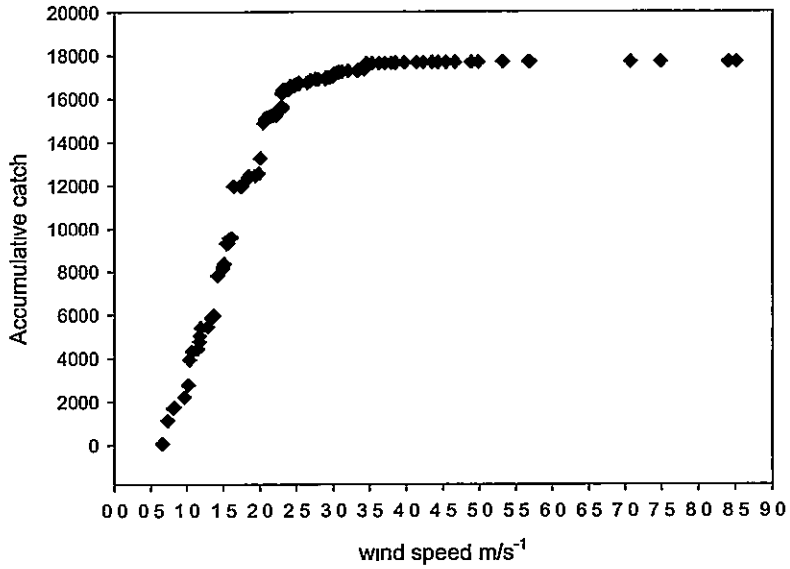

Figure 4-11 Accumulation curve based on spider catches from single days (averages for several days removed) and average wind speed between sun rise and sun set

4.3.2.2 Aerial and ground populations of linyphiids

To assess whether numbers of spiders dispersing are a function of changes in ground population, the influence of daily differences in wind speed were minimised by only considering days with similar average wind conditions. Days or periods with an average wind speed above the median value of 2 356 m/s were discarded as this approximated to the point on the accumulation curve (Figure 4-11) where a clear change in the accumulation rate was evident. This also accounted numerically for half the samples in the subset Correlations between aerial and ground populations were performed on the average of the numbers caught in the climbing-stick samples on days with wind speeds below the 2.356 m/s threshold. Spiders in traps summed over a period of days with favourable ballooning conditions and small numbers dispersing daily, could appear quantitatively similar to summed spiders collected over a number of days where opportunities to balloon were fewer but number of potentially dispersing spiders were

greater. To prevent this possible ambiguity averages were used instead of totals. A log (n+1) transformation was applied to data prior to performing correlations.

4.3.2.2.1. Oedothorax fuscus

Oedothorax fuscus was the most abundant species in the ground and aerial samples with the largest peaks in dispersal occurring in the autumn and winter months. Within the subset of samples, timing of dispersal in males (Figure 4-12) and females (Figure 4-13) appeared to differ in 2003/2004 but was concurrent in 2004/2005. A peak dispersal of males occurred in October/November in both years whilst females peaked in February/March and in November/December of 2004. In February 2004, the peak in dispersing females corresponded to relatively high ground densities. Numbers of females in traps fell sharply in March prior to ground populations declining between April and May. Ground populations of males showed similar variation. Apart from a small rise in June, ground densities of both sexes did not increase markedly until September. Ground densities then declined somewhat before numbers of male and females in traps increased to their highest number in November. No significant correlation was observed between ground densities and average numbers in climbing-stick traps for males. A positive relationship was significant for females ($r = 0.881$, P = 0.004) and total numbers ($r = 0.901$, P=0.002).

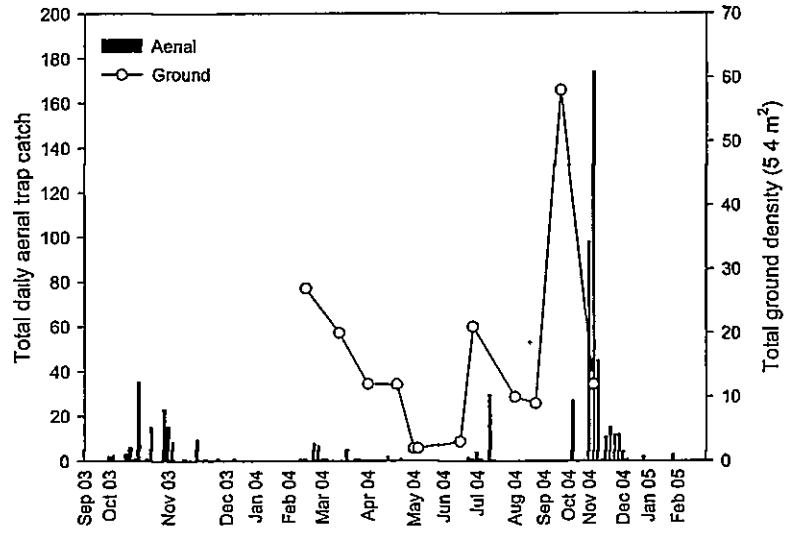

Figure 4-12 Total numbers of *O fuscus* males collected in climbing stick traps (Aerial - bars) and in G-vac samples (Ground - line) Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change.

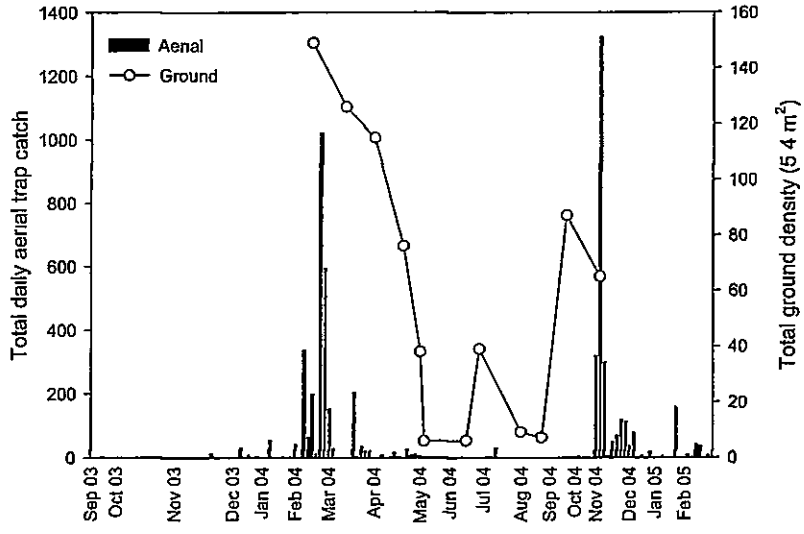

Figure 4-13 Total numbers of *O fuscus* females collected in climbing stick traps (Aerial - bars) and in G-vac samples (Ground - line). Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change

4.3.2.2.2. Oedothorax retusus

The dispersal of *O. retusus* (Figure 4-14, Figure 4-15) reflected that of *O. fuscus* with a peak dispersal of females occurring in February/March and again in November/December in 2004. Compared to *O. fuscus* differences in male and female dispersal was less apparent in 2003/2004 as no distinct dispersal peak was evident for males. Dispersal times for both sexes were concurrent in November/December 2004. The relationship between ground and average numbers in climbing-stick traps was only significant for *O. retusus* females ($r = 0.719$, $P = 0.045$).

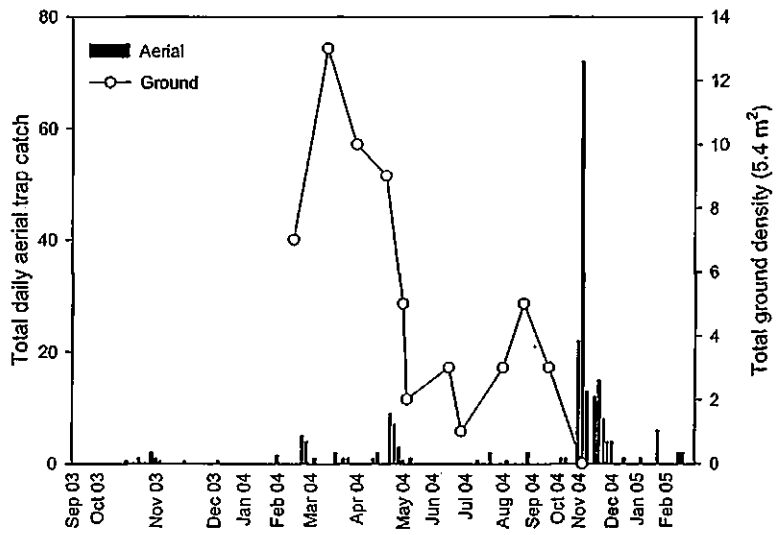

Figure 4-14. Total numbers of *O. retusus* males collected in climbing stick traps (Aerial – bars) and in G-vac samples (Ground - line). Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change.

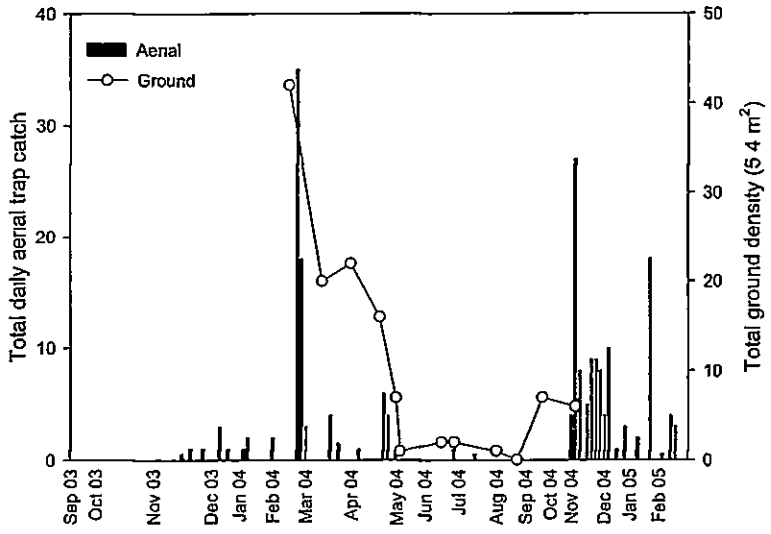

Figure 4-15 Total numbers of *O retusus* females collected in climbing stick traps (Aerial - bars) and in G-vac samples (Ground - line) Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change

4.3.2.2.3. Erigone atra

In contrast to *O fuscus* and *O retusus*, the timing of the major dispersal of *E. atra* males (Figure 4-16) and females (Figure 4-17) followed a similar pattern in both the autumn/winter periods *E atra* was the most frequent disperser of all the spiders identified and both figures display a rather prolonged period of relatively higher dispersal occurring in the autumn/winter but with smaller numbers dispersing throughout the spring and summer No significant relationship was observed between ground densities and average numbers in climbing-stick traps for either males or females.

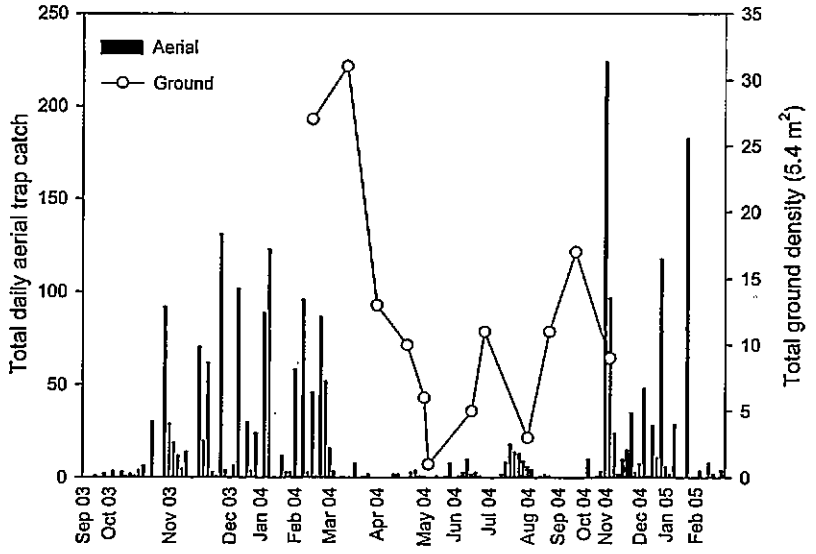

Figure 4-16. Total numbers of *E. atra* males collected in climbing stick traps (Aerial - bars) and in G-vac samples (Ground - line). Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change.

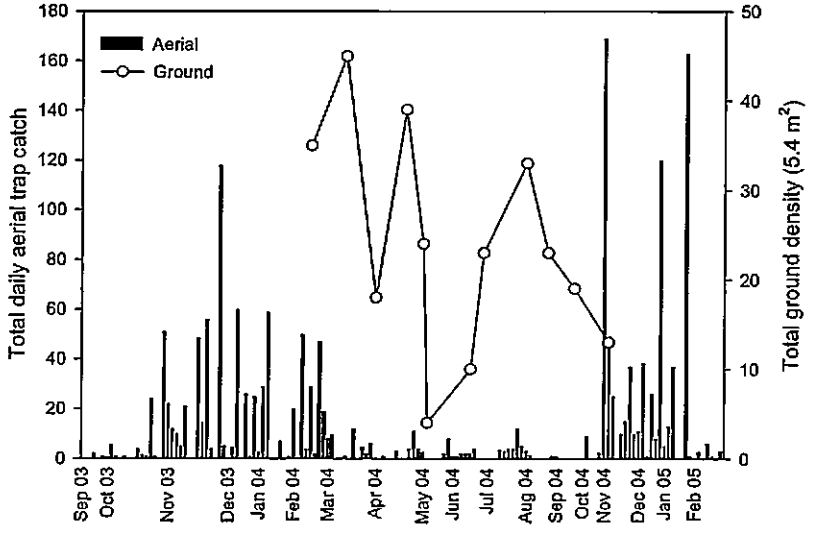

Figure 4-17. Total numbers of *E. atra* females collected in climbing stick traps (Aerial - bars) and in G-vac samples (Ground - line). Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change.

4.3.2.2.4. Erigone dentipalpis

A similar dispersal pattern to *E. atra* was observed for *E. dentipalpis* males (Figure 4-18 and females (Figure 4-19) with a relatively prolonged period of higher dispersal in the autumn and winter and lower but frequent dispersal activity occurring throughout the spring and summer For *E dentipalpis* males a significant positive relationship (r = 0.786, P = 0 021) was observed between ground densities and average numbers in climbing-sticks.

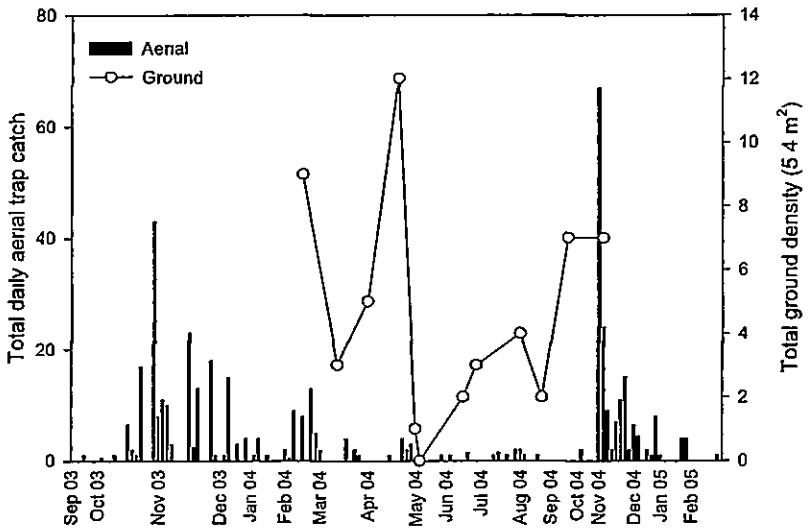

Figure 4-18 Total numbers of *E dentipalpis* males collected in climbing stick traps (Aerial - bars) and in G-vac samples (Ground - line). Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change

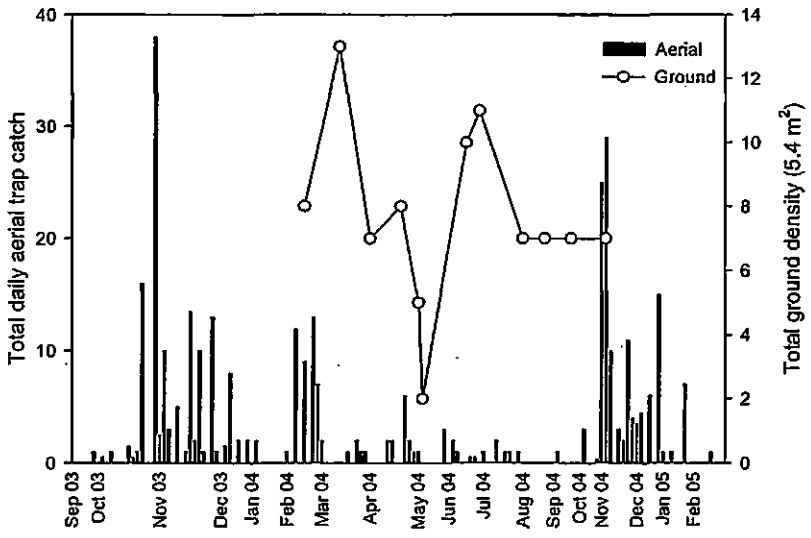

Figure 4-19. Total numbers of *E. dentipalpis* females collected in climbing stick traps (Aerial – bars) and in G-vac samples (Ground - line). Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change.

4.3.2.2.5. Milleriana inerrans

The major dispersal period of males (Figure 4-20) and females (Figure 4-21) occurred in autumn/winter, between November and March although a distinct but smaller period of dispersal was apparent in May/June. Numbers and timing of dispersing males and females corresponded closely. Although both ground density and numbers in traps were high in February, a lack of aerial activity was evident in March/April despite high ground densities persisting up until 21st April. No significant relationship was observed for between ground densities and average numbers in climbing-stick traps.

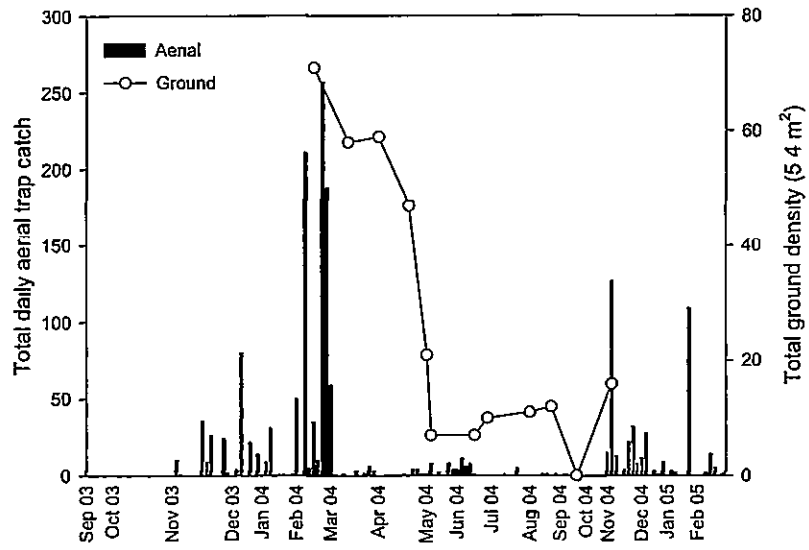

Figure 4-20. Total numbers of *M merrans* males collected in climbing stick traps (Aerial – bars) and in G-vac samples (Ground - line) Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change

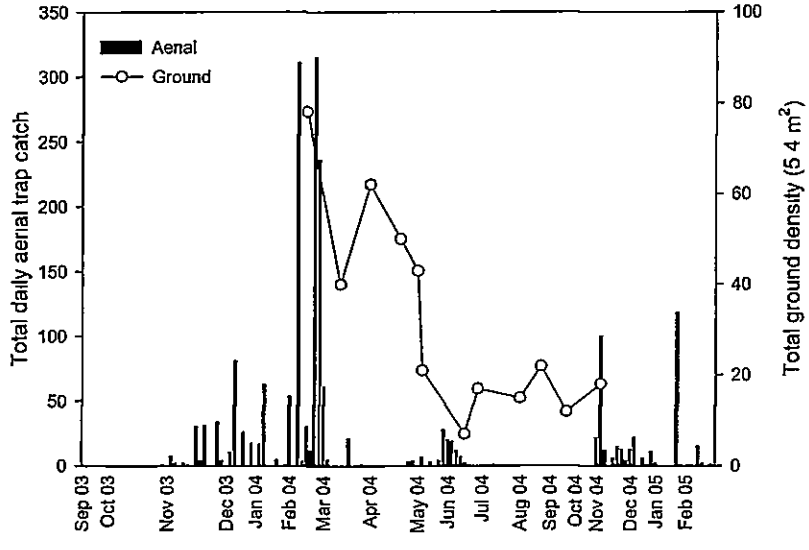

Figure 4-21 Total numbers of *M merrans* females collected in climbing stick traps (Aerial – bars) and in G-vac samples (Ground - line) Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change

4.3.2.2.6. Savignia frontata

Ground densities of *S. frontata* males (Figure 4-22) and females (Figure 4-23) were typically low for this species which was found relatively infrequently in G-vac samples. Higher numbers were caught in climbing-stick traps in the autumn/winter period of both years.

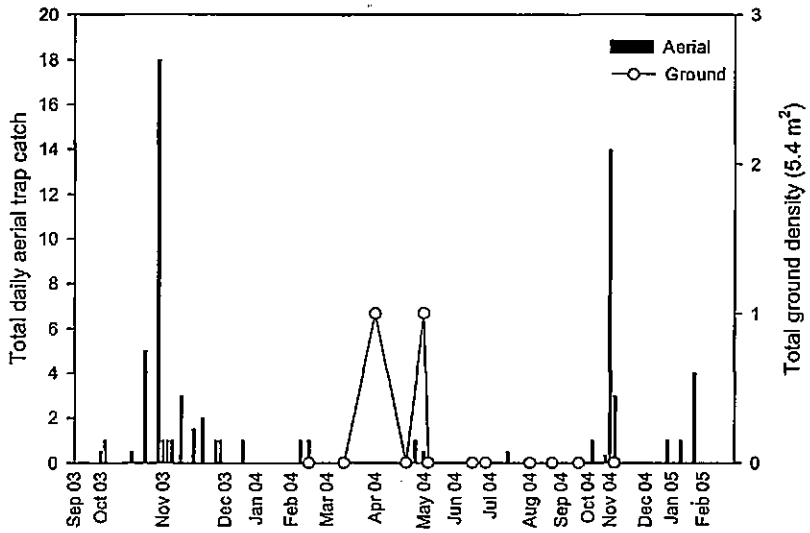

Figure 4-22. Total numbers of *S. frontata* males collected in climbing stick traps (Aerial – bars) and in G-vac samples (Ground - line). Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change.

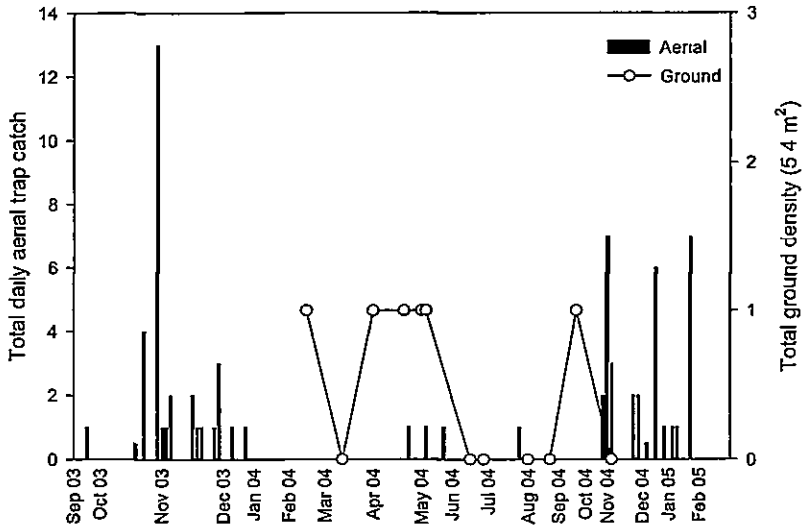

Figure 4-23 Total numbers of *S frontata* females collected in climbing stick traps (Aerial – bars) and in G-vac samples (Ground - line) Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change

4.3.2.2.7. Tenuiphantes tenuis

Numbers of male (Figure 4-24) and female (Figure 4-25) *T tenuis* in climbing-stick traps peaked in the autumn/winter periods in both years and appeared to correspond closely in timing Between February and May, males and females were absent from climbing-stick traps although low numbers were caught frequently from May A large peak in ground density was observed in July/August which was not reflected in an increase in numbers caught in traps No significant relationship was observed between ground densities and average numbers in climbing-stick traps

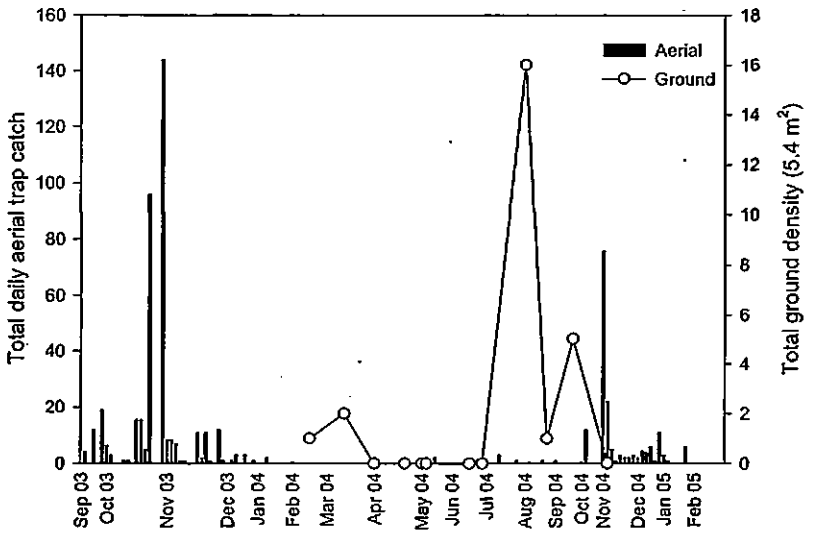

Figure 4-24. Total numbers of *T. tenuis* males collected in climbing stick traps (Aerial – bars) and in G-vac samples (Ground - line). Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change.

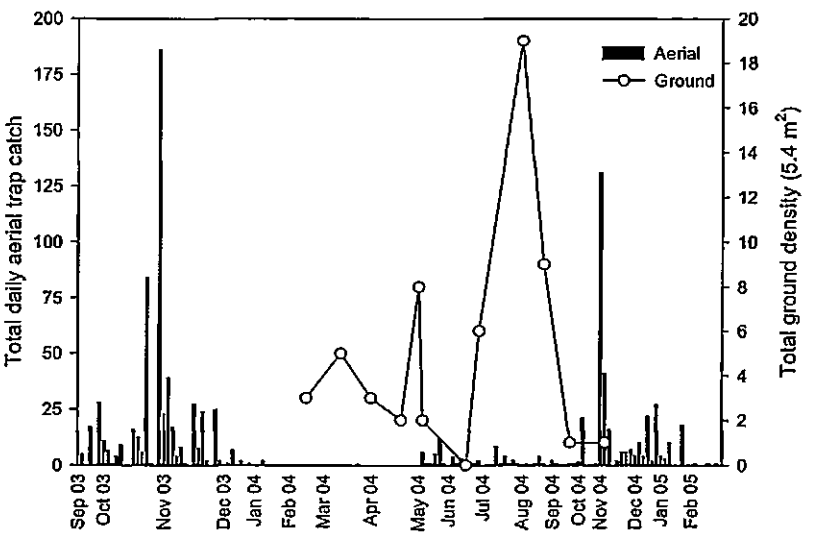

Figure 4-25. Total numbers of *T. tenuis* females collected in climbing stick traps (Aerial – bars) and in G-vac samples (Ground - line). Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change.

4.3.2.2.8. Bathyphantes gracilis

The pattern of dispersal of male (Figure 4-26) and female (Figure 4-27) *B. gracilis* was similar to that of *T. tenuis* with peak dispersal in autumn/winter and a near absence of spiders caught in traps between February and May, but with low but frequent dispersal recorded thereafter A peak in ground population was observed in April and again in July/August which corresponded to the peak in *T. tenuis*. These increases were not reflected in increased numbers in the climbing-stick traps and for *B gracilis* males a significant negative relationship was observed (r = -0.732, P = 0.039)

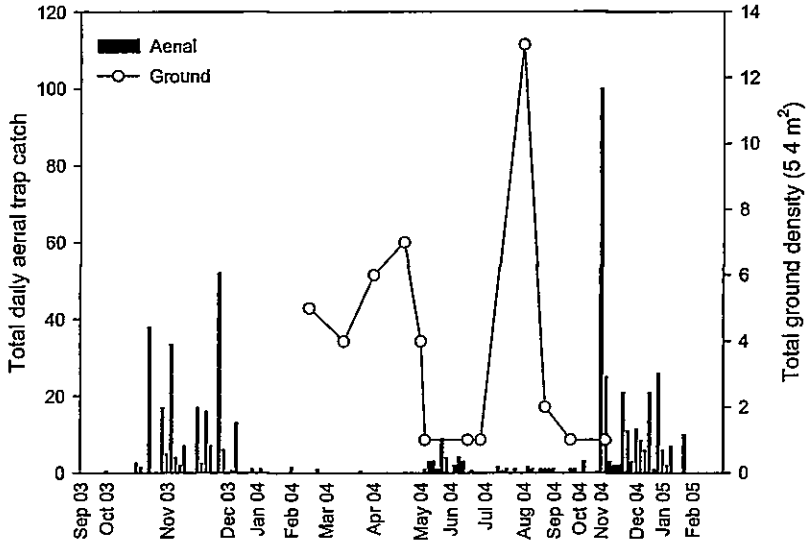

Figure 4-26 Total numbers of *B gracilis* males collected in climbing stick traps (Aerial – bars) and in G-vac samples (Ground - line) Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change

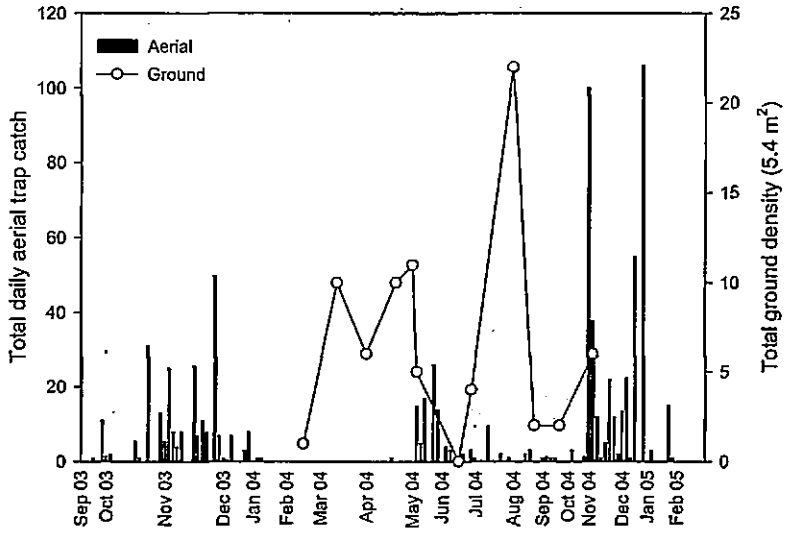

Figure 4-27. Total numbers of *B. gracilis* females collected in climbing stick traps (Aerial – bars) and in G-vac samples (Ground - line). Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change.

4.3.2.2.9. Adult and immature linyphiids

Immature linyphiids (Figure 4-28) were caught frequently in traps throughout the year but were generally less numerous than adults. Numbers in traps decreased in March/April and increased between May and July. Another decrease was seen from August to October which coincided with a large increase in ground densities. An increase in both the number and frequency in traps was evident between November and January of 2004/2005. No significant relationship was observed between ground densities and numbers in climbing-stick traps.

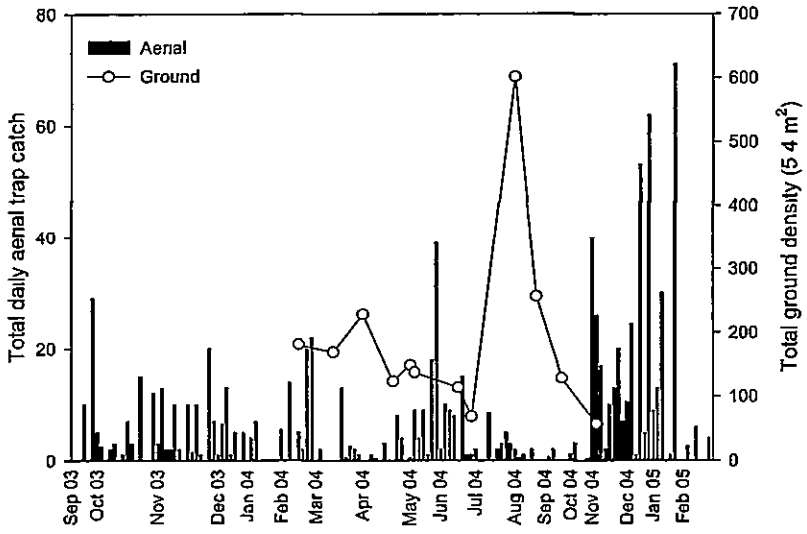

Figure 4-28 Total numbers of immature linyphiids collected in climbing stick traps (Aerial – bars) and in G-vac samples (Ground - line) Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change

Combining the catches of all adult linyphiids (Figure 4-29) caught in climbing-stick traps reveals that for common agrobiont species, autumn and winter represent the time of greatest dispersal activity Fewer numbers are seen dispersing in the spring and summer period although frequent dispersal continues No significant relationship was observed between ground densities and numbers in climbing-stick traps.

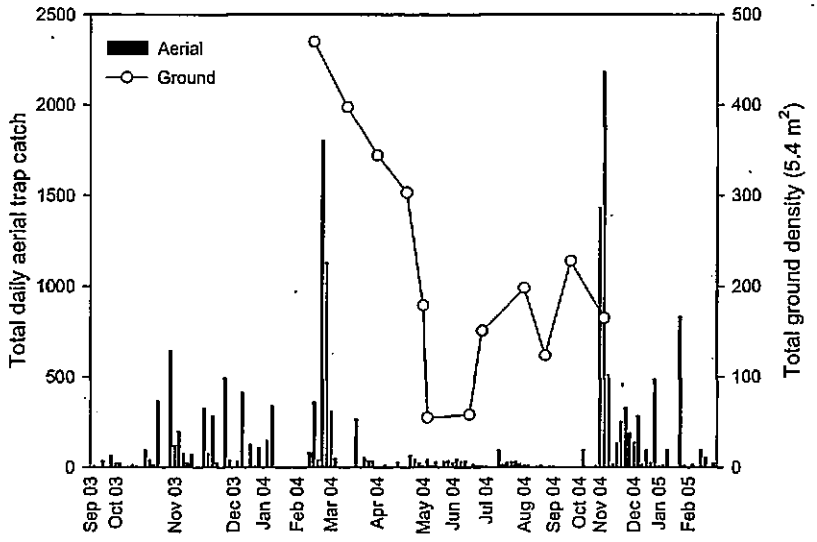

Figure 4-29. Total numbers of adult linyphiids collected in climbing stick traps (Aerial – bars) and in G-vac samples (Ground - line). Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change.

4.3.2.3 Aerial and ground populations of other species

Non-linphiid species caught in climbing-stick traps were represented by the following families-

Araneidae	Lycosidae	Tetragnathidae
Clubionidae	Mimetidae	Theridiidae
Dictynidae	Pisauridae	Thomisidae

Not all specimens caught can be said to have climbed into traps with the intention of ballooning, but as many represent non-agrobiont species, not found typically in the open field environment, then it is likely a substantial proportion were actively dispersing. Immature thomisids and lycosids were present in the field and caught frequently in traps between August to November although a peak in immature lycosid numbers was also present in April. Adults of both families were rarely caught. Lack of defining characters

made identification of immatures problematic, but the following species dispersed as adults and were positively identified

4.3.2.3.1. Robertus arundineti

Although *R arundineti* (Figure 4-30 and Figure 4-31) is regarded as being 'uncommon' (Roberts 1993), this species occurred frequently in climbing-stick traps. Ground densities were low though previous sampling with the D-vac had collected this species on several occasions. Dispersal activity occurred in autumn/winter and extended into spring No dispersal activity was evident between June and late October. Locket and Millidge (1953) describe *R arundineti* as a "rare" spider frequenting "heather and grass on open moor and mountain sides" The proximately of Dartmoor to the west and lowland heaths to the north may account for the local abundance of this species however Samu and Szinetar (2002) also found *R arundineti* frequently on arable land Another spider of the genus *Robertus*, *R. neglectus* (O P.-Cambridge), occurred in the traps in smaller numbers but contrasted in dispersal activity with the majority of specimens being caught between July and September *Robertus lividus* (Blackwall) which is "by far the commonest species [in the genus]" according to Roberts (1993), was not present in either ground or aerial samples although small numbers have previously been recorded in D-vac samples.

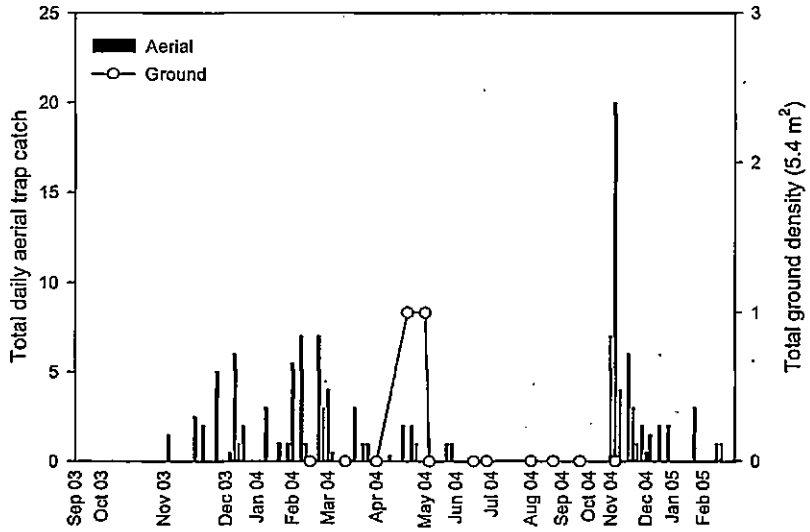

Figure 4-30. Total numbers of *R. arundineti* males collected in climbing stick traps (Aerial - bars) and in G-vac samples (Ground - line). Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change.

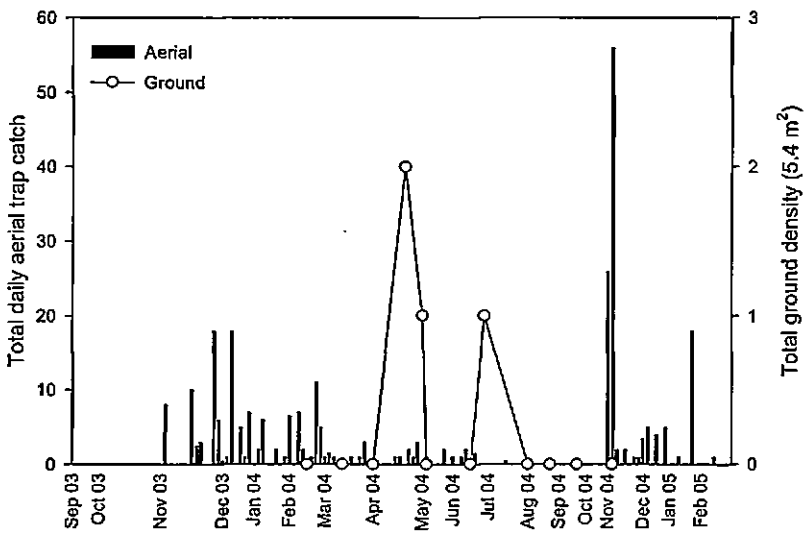

Figure 4-31. Total numbers of *R. arundineti* females collected in climbing stick traps (Aerial - bars) and in G-vac samples (Ground - line). Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change.

4.3.2.3.2. Pachygnatha degeeri

Pachygnatha degeeri (Figure 4-32 and Figure 4-33) is a common and widespread species and is beneficial in being predacious on aphids (Harwood, Sunderland *et al* 2005). Immature spiders make small orb-webs close to the ground but change to a wandering habit as adults (Roberts 1993) The spider was present in moderate numbers in both ground samples and climbing-stick traps Dispersal times appear to be well defined in both sexes occurring between October and December. In the intervening period, when most of the ground population samples were taken, there is a complete absence of dispersal activity Ground populations were for the most part recorded in this period and so information is lacking on their relative abundance during dispersal periods In 2004 the beginning of dispersal activity in October/November did not appear to be associated with an increase in ground density D-vac samples taken over the longer period also did not show ground density to be consistent with numbers caught in traps, with the only peak in ground density occurring in June/July

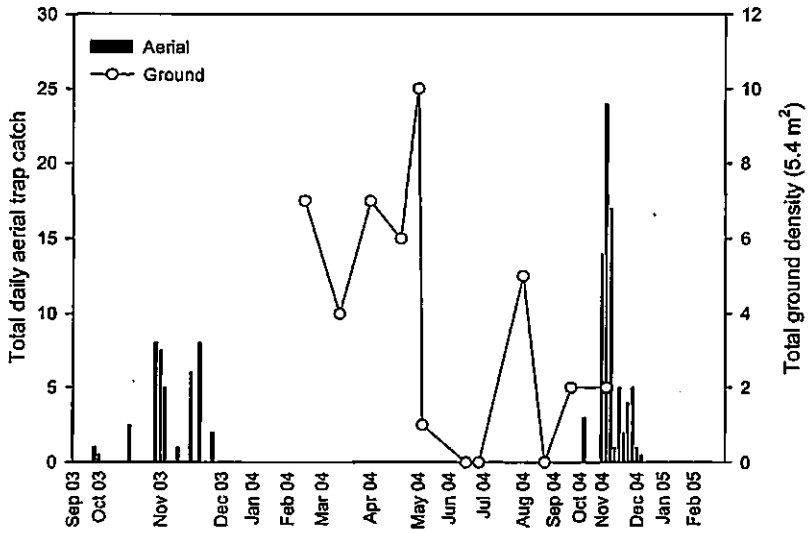

Figure 4-32. Total numbers of *P. degeeri* males collected in climbing stick traps (Aerial – bars) and in G-vac samples (Ground - line). Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change.

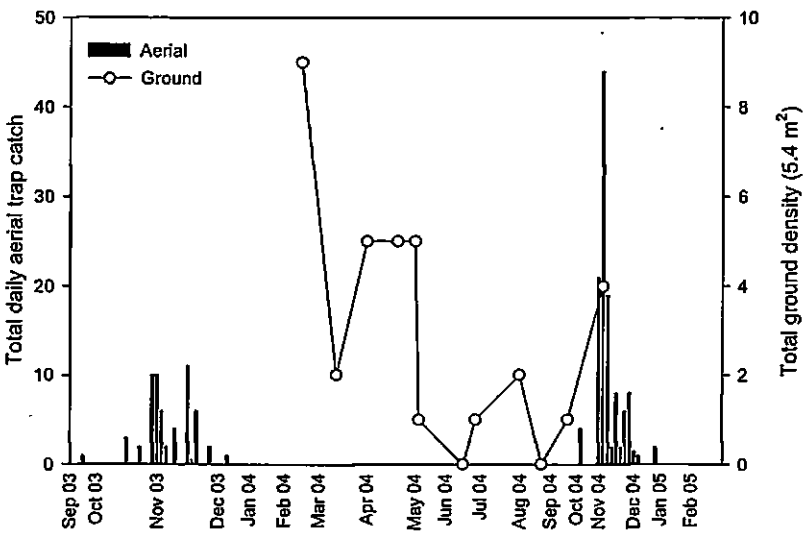

Figure 4-33. Total numbers of *P. degeeri* females collected in climbing stick traps (Aerial – bars) and in G-vac samples (Ground - line). Dates along the x axis are not scaled to time other than in chronological order and the line between points is for clarity only and not proportional to a consistent rate of change.

4.3.2.4 Sex ratios of aerial and ground populations

Ground population samples of all species, apart from *P degeeri*, were dominated by females (Table 4-2). For most species this was reflected in the aerial population with the exception of *E. atra*, *E. dentipalpis* and *O. retusus* where male ballooners were more numerous Sex ratios of the *Erigone* species were very similar in proportion in both aerial and ground samples *Oedothorax* species were in contrast dissimilar with *O. retusus* displaying relatively more ballooning males. *O fuscus* numbers were heavily dominated by females in both ground and aerial samples Females of *B gracilis* and *T. tenuis* dominated in both samples but to a lesser degree and females of *M merrans* only moderately exceeded males in aerial and ground samples.

Table 4-2 Total numbers of males in females caught in climbing-stick traps (Aerial) and G-vac sample and corresponding ratios of male to females

	Aerial			Ground		
Species	male	female	ratio	male	female	ratio
E atra	2594	1908	1 36	144	286	0 50
E dentipalpis	507	390	1 30	55	92	0 60
O fuscus	713	6019	0 12	188	723	0 26
O retusus	226	221	1 02	61	126	0 48
B gracilis	632	900	0 70	79	125	0 63
T tenuis	660	1165	0 57	25	59	0 42
M merrans	1735	2016	0 86	319	385	0 83
S frontata	73	79	0 92	2	6	0 33
R arundineti	134	316	0 42	4	6	0 67
P degeeri	141	210	0 67	44	35	1 26

4.4 Discussion

In comparison to the study by Weyman *et al.* (1995), fewer correlations were observed between the aerial and ground densities. Only numbers in climbing-stick traps of *Oedothorax* females and *E. dentipalpis* males were positively associated with ground populations and catches of *B. gracilis* males were negatively associated. This may be due to the different methods used for sampling ballooning spiders with deposition traps being more selective at sampling local populations than climbing-stick traps. Spiders in the vicinity of a deposition trap may climb the frame and fall into the trapping solution whilst attempting to balloon (C.F.G. Thomas pers. comm.). In this respect both methods are similar in that the climbing-sticks have a net cone guiding climbing spiders to the trap above (Woolley, Thomas *et al.* 2007). The interception areas of each method differ however. The interception area of a deposition trap is the horizontal edge of the frame on the windward side and the trays containing the trapping solution. Spiders intercepted by the edge (in the same manner as a wire fence) have a possibility of being trapped when attempting to balloon off again from the trap's edge. The probability of spiders falling directly into the trapping solution may be less likely owing to the 'glancing angle' of the horizontal surface area of the solution in relation to the prevailing lateral movement of the wind. Both the actual 'interception area' and the trapping potential of that area therefore may be hard to calculate beyond the edge length (1.2 m in the deposition traps) as this may vary accordingly with different wind conditions. The sloping net of a climbing-stick trap exposes in a single direction an effective area of 0.5 m^2, ten traps being equivalent to a net with sides of 2.24 x 2.24 m. The low angle of incidence of this surface result in spiders having a greater chance of being intercepted whilst airborne and therefore catches may reflect the wider population of spiders outside the field in which the traps are placed. In addition to this, the difference between aerial

and ground samples may have been exacerbated by within-field operations such as the silage cut in May Although ground population sampling extended into November 2004, ballooning activity occurring later than this could not be compared owing to the absence of ground data and therefore the overall comparison was perhaps limited by this omission.

The high efficiency of the traps, although limiting ground comparison, was arguably more appropriate for describing dispersal patterns of different species independent of local within-field factors. Although the total caught (22,704) represent only a quarter of samples (one week per month) collected over the period, the subset being equivalent for all species, allows for a direct comparison of relative ballooning activity, on each day, for species and sexes

Comparing dispersal activity between males and females, of particular note was the incidence of dispersing male and non-dispersing female *O fuscus* in October 2003 D-vac samples (not shown) indicated ground densities of *O. fuscus* females to be relatively high in October yet this was not reflected in females being caught in climbing-stick traps. The timing of peak dispersal in males was similar in 2003 and 2004. Wind speeds (Figure 4-10) were however relatively higher during October 2003 than those recorded during the following peak in November 2004 Although females showed very little dispersal in October 2003, dispersal activity was seen to peak later during the period of lower wind speeds in February and March 2004. In both years the pattern of dispersal activity appears to suggest meteorologically induced peak dispersal for females but for males, an additional stimulus appears to be of relevance inducing dispersal under conditions where female dispersal is not stimulated

The year 2003 was exceptional in respect to temperature, with extremes (highest recorded temperature of 38.5 °C in Kent in August) and an eight month spell of continuous above average monthly temperatures from February to September (Met office monthly summary - http://www.metoffice.gov.uk/climate/uk/2003/). Drought conditions were also prevalent with February to October being the driest period since 1921 (Marsh 2004). The local consequences of these dry conditions were not known although with respect to prey availability, numbers of springtails were observed to collapse during the dry summers of 1975 and 1976 on farmland in Sussex (Aebischer 1990). Stress through lack of prey availability tends to increase dispersal tendency (Thomas and Jepson 1999; Weyman, Sunderland *et al.* 1994; Wingerden van and Vugts 1979) though whether this could independently promote dispersal in male spiders is not known, but seems unlikely as food intake is normally far higher in egg-producing females (De Keer and Maelfait 1987a). Indeed, Bonte *et al.* (2009) have shown that sex differences are apparent when nutrition is limited with ballooning propensity in *E. dentipalis* and *Erigone arctica* being enhanced in females but suppressed in males.

Another limitation for males may be the lack of mating opportunities. Male spiders maturing late in the season would be at a particular disadvantage in this respect, females having already mated thus lowering the probability of paternity for subsequent mates. In the closely related species, *Oedothorax retusus,* a male strategy is to produce mating plugs; secretions which may block the genital opening or tract after copulation thus preventing females from remating (Uhl and Busch 2009). Whether *O. fuscus* males use a similar strategy is unknown. Reproductive success may be further limited by time as conditions deteriorate towards winter. Males also are not as long-lived as females and the over-wintering population of *O. fuscus* consists largely of gravid females inseminated in the autumn (De Keer and Maelfait 1987a; De Keer and Maelfait 1987b).

It is not known whether male spiders are behaviourally responsive to this closing window of mating opportunity and their own reproductive history. Greater ballooning propensity may however occur if the time cost and risk of ballooning is offset by increasing the likelihood and/or number of successful matings Heightened ground activity of male *O fuscus* in October has been correlated with male-only catches in window-traps (De Keer and Maelfait 1987b) Whilst these observations may be related to mate-searching, without further knowledge of a male's physiology and mated or unmated status, it cannot be said whether male-only ballooning is a facet of mate-searching strategy or coincidental to it. At present little work has been undertaken on ballooning propensity regarding the mated or unmated status of spiders. In a recent study, wind chamber experiments revealed no difference in ballooning propensity for mated and unmated female *E atra* (Bonte, De Clercq *et al* 2009) As yet no similar work has been published on male spiders.

Other explanations for male-only dispersal could be that males become accidentally airborne whilst mate-searching, perhaps when rigging over vegetation That spiders in this study climbed to the top of 1 2 m climbing-sticks, suggests however that airborne dispersal was intended. Alternatively, if greater activity by males whilst mate-searching can be assumed, a specific 'reproduction related' cause may not be required if increased activity causes a physiological threshold to be exceeded where pre-ballooning activity is triggered or is more likely to occur. For instance if male spiders are more exposed to radiative heating whilst searching, or higher temperatures are generated internally through cursorial movement, then a possible physiological precursor to pre-ballooning behaviour, such as an increase in body temperature, could be achieved.

Regarding both *O. fuscus and O. retusus* females, the larger peaks in aerial activity (e.g. Figure 4-13) appear to coincide with prolonged periods of relatively low wind speeds. The peaks were evident in February 2004 and in November/December 2004 when median winds over the sample period were lowest (Figure 4-10). This is somewhat in contrast to the dispersal pattern of the *Erigone* species which appear to balloon more frequently (e.g. Figure 4-16) although within the upper wind speed threshold. Cumulative catch curves for both *Erigone* and *Oedothorax* were very similar to the total cumulative catch in relation to wind speed (Figure 4-11). That *Erigone* species are observed to balloon more frequently than *O. fuscus* is confirmed by several other studies (Thomas and Jepson 1999; Weyman, Sunderland *et al.* 2002). A further analysis of the data may indicate whether *Oedothorax* dispersal activity is related to either low wind speed, the relative difference in wind speeds below a certain threshold, the length of the low wind speed period or associated factors. In comparison with *Erigone* species, the rather 'choosy' nature of *Oedothorax* may be expressed in these spiders utilising longer favourable weather windows enabling spiders more time to disperse again before the ballooning tendency is turned off by inhibiting weather conditions. Whether spiders can detect and react to favourable conditions immediately or need a certain 'priming' period is unclear. On a day-to-day basis, wind speeds show some positive correlation although at mid latitudes the hourly autocorrelation function reaches zero values after approximately 36 hours (Brett and Tuller 1991). Temporal autocorrelation may however increase in slow-moving stable anti-cyclonic weather systems associated with ballooning (Thomas and Brain 2003) and therefore a period of very low winds could be a predictor for a longer spell of suitable ballooning conditions. Why *Erigone* and *Oedothorax* appear to have different strategies may relate to the stability of ancestral habitats and/or behavioural differences. For example *Oedothorax* species, in not making webs, are perhaps more inclined to disperse cursorially to better feeding sites than

Erigone species Weyman *et al* (2002) remark that the greater frequency in ballooning in *E. atra* may relate to these species being better adapted to ephemeral habitats as is supported by *E. atra*'s increased reproductive efficiency at low prey densities and lower mortality (De Keer and Maelfait 1988b) Although both species are abundant in crops, the high percentage of grazing land compared with arable land at the study site could benefit *O fuscus* in providing a greater proportion of habitats which are only partially disturbed by grazing A less active dispersal strategy could be beneficial in this environment in reducing dispersal related mortality

Tenuiphantes tenuis and *B. gracilis* display similar ballooning patterns In both species there is a conspicuous absence of ballooning from January to May Relatively small numbers were recorded thereafter till November for *T. tenuis*, but a peak in ballooning was evident for *B gracilis* in May/June. Despite favourable ballooning conditions in February and March, no ballooning was recorded even though adults were present in ground samples However, apart from the population peak in July/August, which was observed in both species, ground densities were not especially high throughout the year compared to the common erigonids. The lack of ballooning in the earlier months is supported by the very low ground densities observed by Topping and Sunderland (1998) prior to May in winter wheat and may be synonymous with low densities of these species in general before May Grazed grass ley, not being the preferred habitat particularly for *T tenuis*, may account for the low numbers ballooning after May and the lack of synchronicity with ground samples. The lack of local selectivity of the traps and the silage harvest in May are also confounding factors. The low number of adults of *T tenuis* and *B. gracilis* ballooning after December could relate to either low numbers of adults moving out of non-crop habitats or to mortality such that the majority of migrants from non-crop habitats in the new year are immatures. The peak ballooning of

B. gracilis and *T. tenuis* in November/December is consistent with low wind speeds in this period. However in the previous year, the peak dispersal period occurred earlier in October/November when wind speeds were relatively high. The cause of this is unknown but poor habitat quality in relation to the dry conditions in 2003 may be of significance.

Both sexes of *M. inerrans* showed very consistent dispersal patterns. The major dispersal activity occurred between November and March although the small peak in May/June was similar to that seen for *B. gracilis* and could indicate increasing ground densities of adults consistent with the maturation of first generation spiders.

Although immature *P. degeeri* were found frequently in ground samples, they were only caught rarely (7 in total) in climbing-stick traps, and therefore the tendency to balloon in this species may only be prevalent in adults. This also could be related to their behavioural shift from web spinning as immatures to a cursorial hunting habit as adults (Roberts 1995). The ballooning time were very constrained in both years being between October and November. From the ground data for females (Figure 4-33) this appeared to coincide with increased densities. Although adults were present outside these ballooning periods, lack of data on ground densities in the wider landscape makes it unclear whether this is a ground density effect or whether dispersal may be mediated through other means.

The ground populations of most linyphiids species were dominated by females. The ratio of females to males in *O. fuscus* was very pronounced (4:1 in ground samples and 8:1 in aerial samples). De Keer and Maelfait (1987b) remark that *Oedothorax* species were quite untypical of other linyphiids in having more females caught in pitfall traps

than males, as it usually the case. This was explained by both sexes' cursorial habit and so the pitfall data might not be biased and supports similar findings in this study. As regards ballooning spiders, Duffey (1956) found that in most species females dominated catches. These findings however differ for *Erigone* species which in the present study were dominated by males. Also of interest is the discrepancy between the sex ratio of *Oedothorax* species in climbing-stick traps. Ground populations were both dominated by females but in climbing-stick traps this ratio increased in *O.fuscus* and decreased in *O retusus* such that numbers of males and females ballooning were approximately equal. Rather variable accounts of sex-ratios have been given in the literature which may partially be the result of small samples and short-trapping times which do not accurately describe overall propensity as each sex may be relative more abundant in samples at different times of year (Weyman, Sunderland *et al* 2002).

Ballooning behaviour in the wind chamber between *E. atra* and *O. fuscus* shows a marked contrast (Figure 4-4, Figure 4-5) with pre-ballooning behaviour being elicited readily in *E atra* and negligible pre-ballooning behaviour occurring in *O fuscus* Greater ballooning frequency in *E atra* (Figure 4-17) is observed in the field compared to *O fuscus* (Figure 4-13) That the wind chamber more readily stimulated pre-ballooning in *E atra* through low wind speeds could indicate that in contrast a more complex set of prerequisite conditions are necessary to elicit ballooning in *O. fuscus* These could either be other abiotic factors not replicated in the wind chamber, or that a longer duration of exposure to low wind conditions is required to stimulate ballooning activity To determine whether different airflow characteristics may produce a different pre-ballooning response, several *O. fuscus* were placed in a chamber similar to that used by Weyman *et al* (1995) with a vertical airflow No difference in the inclination to balloon was observed under vertical airflow conditions (C. Woolley unpublished).

In contrast to findings of Weyman *et al.* (1995) for *Erigone* spp., *E. atra*, females did not show a consistent ballooning response over the period of the study (Figure 4-6). More time spent in pre-ballooning behaviour and lower latencies (although these variables are not independent) were observed in later months (Figure 4-6, Figure 4-7). This pattern however was not reflected in field observations for the same months in the previous year (Figure 4-17) and no clear pattern was discernable for males (Figure 4-8, Figure 4-9) in the wind chamber. That spiders were kept outside in a shaded area could be of some significance for the activity observed in *E. atra* females. Without radiative warming by the sun, spiders may not have been sufficiently warmed before being placed in the wind chamber. In warmer months spiders were consequently more active and exhibited greater ballooning propensity.

Along with a male *Hyptiotes paradoxus* (C. L. Koch) caught during field testing of the climbing-stick traps (Smithers 2004), a number of other scarce species were also collected in small numbers (*Philodromus albidus* Kulczynsk, *Mioxena blanda* (Simon), *Philodromus collinus* C. L. Koch, *Achaearanea simulans* Thorell) . Although ballooning propensity for specialist spiders in a fragmented habitat is observed to be lower (Bonte, Vandenbroecke *et al.* 2003), the survival value of dispersal in founding new colonies (den Boer 1990) is supported by these observations as is the observation of rare spiders colonising green roof spaces in London (Kadas 2006).

Duffey (1956) suggested breeding activity, population density and weather conditions were important for determining the different dispersal patterns observed in several species. The seasonality suggested by Duffey (1956), at least for *Erigone*, is not supported by the findings of Weyman *et al.* (1995) where ballooning is observed to occur throughout the year and variations in numbers ballooning are primarily a function

of population density The present study partially supports ground densities influencing the degree of seasonal ballooning activity observed Variation between local ground densities and trap catches are likely caused by interception of spiders from the surrounding area. For *O fuscus*, the 'male-only' dispersal peak in October, whilst not suggesting seasonality, may indicate differences in motivation for ballooning in sexually mature adults

Similarity in dispersal activity between closely related species indicates that, although ground populations and a 'mixed response' to ballooning between individuals on a daily basis may be generally appropriate (Bell, Bohan *et al* 2005; Weyman, Jepson *et al.* 1995), common aspects of development and response to environmental stimuli between closely related species may also be influential in producing the 'taxon specific' patterns of dispersal activity observed. Longer term studies would be useful in confirming the degree of variability in these patterns.

Chapter 5. Spider populations on a mixed-farm; an analysis of monitoring results

5.1 Introduction

Starting in 2001, a programme was initiated to sample ground densities of spiders in several crop types over a period of two cropping seasons.

Using the data collected, analyses were conducted for the purpose of :-

i) providing a general description of the community of agrobiont spiders present at the study site;

ii) describing the change in linyphiid abundance over the time series;

iii) exploring patterns in species assemblage to determine whether spider assemblages are uniform or show distinct differences at the field scale that relate to crop/field characteristics (cereals, maize, grass leys and set-aside).

The results are discussed in relation to how field usage and management on a mixed farm provides crop/management-specific resources to spiders over the annual cropping cycle.

5.2 Materials and methods

5.2.1 Sampling

Fields were sampled at 2 to 3 week intervals over a 17 month period from June 2001 to October 2002. Sampling was performed using a D-vac suction sampler (manufactured by Dietrick, US), a comparatively large sampler widely-used previously for sampling spiders in tall crops such as wheat (Thomas and Jepson 1997). The circular nozzle of 0.1 m^2 diameter was lengthened with a 1 metre extension enabling mature cereal crops to be sampled without damage whilst still maintaining a good contact with the ground. In this instance, interval suction samples were deemed a more practical solution than continuous sampling from pitfall traps (which would have required a high level of maintenance due to farming operations, damage by livestock, etc.) This provided a time-effective method to conduct a multiple-field study, both in terms of the time taken to conduct field work and to sort the samples Suction sampling also allowed spot monitoring of populations before and after farming operations (see *Chapter 6*) with results being comparable without correction for unequal sampling periods Samples were required to be taken in dry conditions which unavoidably affected sampling intervals.

On each sample date a total of 6 sub-samples were taken in the central area of each field Each sub-sample consisted of 9 randomly placed applications of the D-vac, each application being a 10 second placement of the nozzle over the crop, onto the ground surface. For all subsequent analysis sub-samples were combined to form a composite sample, the total area sampled being 5.184 m^2. Only species abundance data in fields was collected to fulfil the original remit of the data collection exercise (not discussed in this thesis).

5.2.2 Data handling

The number of sampling days varied for each field - usually to take account of farm operations (see *Chapter 6*). The number of sampling dates were in general, proportional to the required number of operations for each crop. For the analysis of each field over a time series, additional samples taken for monitoring field-specific management were discarded to give a dataset (the adjusted dataset) with equal sampling dates (n = 21). Proportions of spiders relative to the number of sample dates were not used as the distribution of additional sample dates over the year was different for each field. Additional sample dates were included for the Correspondence Analysis (see below).

5.2.2.1 Exploratory techniques

Summary statistics were generated for these data and ranked abundance plots were used to represent species composition. Diversity of each field (Figure 5-2) was calculated using the log series α diversity. The α index is calculated from:

$$\alpha = \frac{N(1-x)}{x}$$

where x is obtained from the iterative solution of

$$S/N = [(1-x)/x] \cdot [-\ln(1-x)]$$

S being the number of species and N the total abundance with x for all fields being in the range of 0.985 to 0.996.

Dominance for each field (Figure 5-2) was calculated using the Simpson Index (D)

$$D = \sum P_i^2$$

As this index gives the lowest value to the highest dominance, it is convention to use the inverse of the index, *1-D*. Equations are taken from Magurran (2004)

In addition, ordination (defined as 'to place items in order') methods were used to explore and assess species composition in different crop types. Ordination, a form of gradient analysis, encompasses a number of techniques with the common aim of reducing the multivariate complexity of the data to a lesser number of 'dimensions' by which major patterns in the dataset can be revealed. Dimensions take the form of axes along which samples are ordered according to the variability in their community composition, the axes describing the greatest variability being generally the most ecologically significant. These axes may describe gradients in some environmental variables and when measured may be correlated with these variables (McGarigal, Cushman *et al.* 2000).

Correspondence analysis (CA) is an unconstrained (indirect) unimodal ordination method which reveals associations between species assemblages and site characteristics (Gotelli and Ellison 2004). The test is appropriate when quantitative variables are not used to investigate the influence of directly measured environmental gradients such as soil moisture, tiller density, altitude etc. Instead, gradients are inferred 'indirectly' from the data matrix using a reciprocal averaging technique This process orders sites along axes which account for the greatest, and then successively the next greatest, amount of variation in the data Such an analysis is said to be 'unconstrained', in that gradients are not predetermined by the inclusion of quantitative explanatory variables The gradients are as a consequence hypothetical, but, should the method be appropriate, and the amount of variation accounted for sufficiently large, then the resulting ordination can suggest the existence of environmental variables which are important in determining the

abundance of species at particular sites (Lepš and Šmilauer 2003). These findings along with knowledge of habitat characteristics can then be used as a basis for further investigation. Generally the most relevant ordination is the ordering of sites/species along the two axes expressing the greatest variation. On the ordination plot, decreasing distance between samples and species is proportional to similarity and corresponds to Chi-squared distance. Correspondence analysis was carried out using the software package CANOCO and the graphics package CanoDraw (ter Braak and Smilauer 2002).

Procrustes analysis, or least-square orthogonal mapping, is a procedure which enables the spatial comparison of corresponding coordinates from two data sets. The procedure requires one set of the coordinate data to act as a reference whilst the other is rotated, reflected and rescaled, as required, to a position which minimizes the sum of squared deviations between the corresponding points. From an ecological perspective, the procedure is useful for comparing ordinations of the same sites from different sets of variables to examine their goodness-of-fit; for example to examine the relationship between the species composition of weeds and invertebrates (Smith, Bohan *et al.* 2008). Ordination of the same sites can be compared to determine the magnitude of change in site characteristics over time to assess natural perturbations or the response to disturbance. The procedure is also useful when comparing the results of different ordination methods (Wentworth and Ulrey 2000). Overall, the aim of the test is similar to that of the Mantel test (Mantel and Valand 1970) although the comparison is performed on the coordinates of the ordinated results and not the underlying proximity matrices (Schneider and Borlund 2007). In this instance Procrustes analysis was used to compare field assemblages between years. Procrustes analysis was performed using the PROcrustean randomization TEST program (PROTEST) (Jackson 1995).

5.3 Results

5.3.1 Assemblage structure, diversity and dominance: general observations

In total, 11,297 spiders were sampled and examined from the 7 fields (Table 5-1). Variation in number of spiders between fields was clearly evident - Backdown (the set-aside field) accounted for the greatest number of spiders sampled over the study period with Pitstones and Glazeparks also having relatively high abundance Both these fields were in wheat, although Pitstones only for the second season. For Pitstones, spider abundance in wheat was over three times greater than when in grass over the same period (July to August). Overall spider abundance in wheat was almost twice that found in grass Abundance of spiders in maize was only slightly above those of the grass leys.

Abundance of linyphiids was greatest in Pitstones and Glazeparks, numbers of adults and immatures being similar for both fields (Table 5-1) For the set-aside field Backdown, non-linyphiids spiders accounted for a far greater proportion of the total spiders sampled than for any other field Total linyphiids recorded from set-aside were similar to the numbers recorded from ley and maize fields. Backdown was also notable for the high number of immatures linyphiids relative to adult numbers. The un-rotated grass leys (Bigfield and Bradmores), despite having lower overall numbers of linyphiids, had higher proportions of immatures to adults compared with cereals and maize.

Of the 21 species in the adjusted data set, *O. fuscus* was the most abundant being dominant in 5 of the 7 fields and having an abundance similar and only second to that of *B gracilis*, in the permanent ley field, Bradmores (Figure 5-1, Table 5-2). Only in the set-aside field Backdown was *O fuscus* ranked in a lower position,

Table 5-1. Abundance and percentage per field of adult and immatures linyphiids, non-linyphiids and total spiders sampled from each field.

Field	Crop 01/02	Adult linyphiids	% per field	Immature linyphiids	% per field	Non-linyphiids	% per field	All spiders	% per field
Backdown	Set-aside	219	7.48	1035	15.27	1236	77.78	2490	22.04
Eastdown	Maize	462	15.78	791	11.67	72	4.58	1325	11.73
Bradmores	Perm. ley	269	9.19	782	11.53	16	1.01	1067	9.44
Bigfield	Temp. ley	284	9.7	984	14.51	12	0.76	1280	11.33
Horse Parks	Barley / Temp. ley	352	12.02	687	10.31	48	3.02	1087	9.62
Pitstones	Temp. ley / Wheat	696	23.77	1281	18.89	62	3.9	2039	18.05
Glazeparks	Wheat	646	22.06	1220	17.99	143	9	2009	17.78
Total		2928		6780		1589		11297	

Table 5-2. Species list in order of abundance. (* indicates species only collected on additional sampling dates and not included in total sum for each field, abundance in brackets).

Abbr. (Fig 5-1)	Species (greatest abundance first)	Set-aside BD	Maize ED	Perm Ley BM	Temp Ley BF	Barley/ Grass HP	Grass/ Wheat PS	Wheat GP	Total
Of	*Oedothorax fuscus* (Blackwall, 1834)	24	161	84	117	131	367	181	1065
Bg	*Bathyphantes gracilis* (Blackwall, 1841)	68	61	94	46	76	80	145	570
Tt	*Tenuiphantes tenuis* (Blackwall, 1852)	75	37	28	19	34	109	144	446
Ea	*Erigone atra* (Blackwall, 1841)	6	46	30	56	46	59	37	280
Ed	*Erigone dentipalpis* (Wider, 1834)	6	69	27	22	41	20	10	195
Mr	*Meioneta rurestris* (C.L. Koch, 1836)	2	13	2	10	8	3	77	115
Mi	*Milleriana inerrans* (O.P.-Cambridge, 1884)	0	47	0	3	4	38	17	109
Or	*Oedothrax retusus* (Westring, 1851)	22	17	2	4	6	11	13	75
Pm	*Porrhomma microphthalmum* (O.P.-Cambridge, 1871)	0	2	0	2	2	3	8	17
Sf	*Savignya frontata* (Blackwall, 1833)	0	3	0	4	4	1	2	14
Cc	*Centromerita concinna* (Thorell, 1875)	6	0	0	0	0	0	0	6
Pp	*Pelecopsis parallela* (Wider, 1834)	3	2	0	0	0	0	1	6
Wv	*Walckenaeria vigilax* (Blackwall, 1853)	0	0	0	0	0	1	5	6
Dn	*Dicymbium nigrum* (Blackwall, 1834)	2	0	0	0	0	1	2	5
Mp	*Microlinyphia pusilla* (Sundevall, 1829)	1	0	0	0	0	2	2	5
P	*Pocadicnemis* spp. Simon, 1884	2	3	0	0	0	0	0	5
Ms	*Micrargus subaequalis* (Westring, 1851)	1	1	1	0	0	1	0	4
Wn	*Walckenaeria nudipalpis* (Westring, 1851)	0	0	0	0	0	0	2	2
Gv	*Gongylidiellum vivum* (O.P.-Cambridge, 1875)	1	0	0	0	0	0	0	1
Hc	*Hypomma cornutum* (Blackwall, 1833)	0	0	1	0	0	0	0	1
Pc	*Porhomma campbelli* F. O. P.-Cambridge, 1894	0	0	0	1	0	0	0	1
Tf	*Tenuiphantes flavipes* (Blackwall, 1854) *	0	0	0	0	0	0	1	(1)
Cb	*Centromerita bicolor* (Blackwall, 1833) *	0	0	0	0	0	0	1	(1)
Db	*Dismodicus bifrons* (Blackwall, 1841) *	0	0	0	0	1	0	0	(1)
	Total adults per field	219	462	269	284	352	696	646	
	Total species per field	14	13	9	11	10	14	15	

T tenuis and *B gracilis* being more numerous Of the four species with the highest abundance, *T. tenuis* and *B gracilis* were found predominately in wheat in Glazeparks whilst *O.fuscus* was more numerous in Pitstones, again with numbers in wheat exceeding those in grass over the same period For *E. atra*, abundance was broadly similar in all fields except for set-aside where very low numbers were sampled Similarly the lowest numbers of *O fuscus* were also sampled from set-aside. Both *T tenuis* and *B gracilis* were recorded in their lowest numbers in the temporary ley field, Bigfield

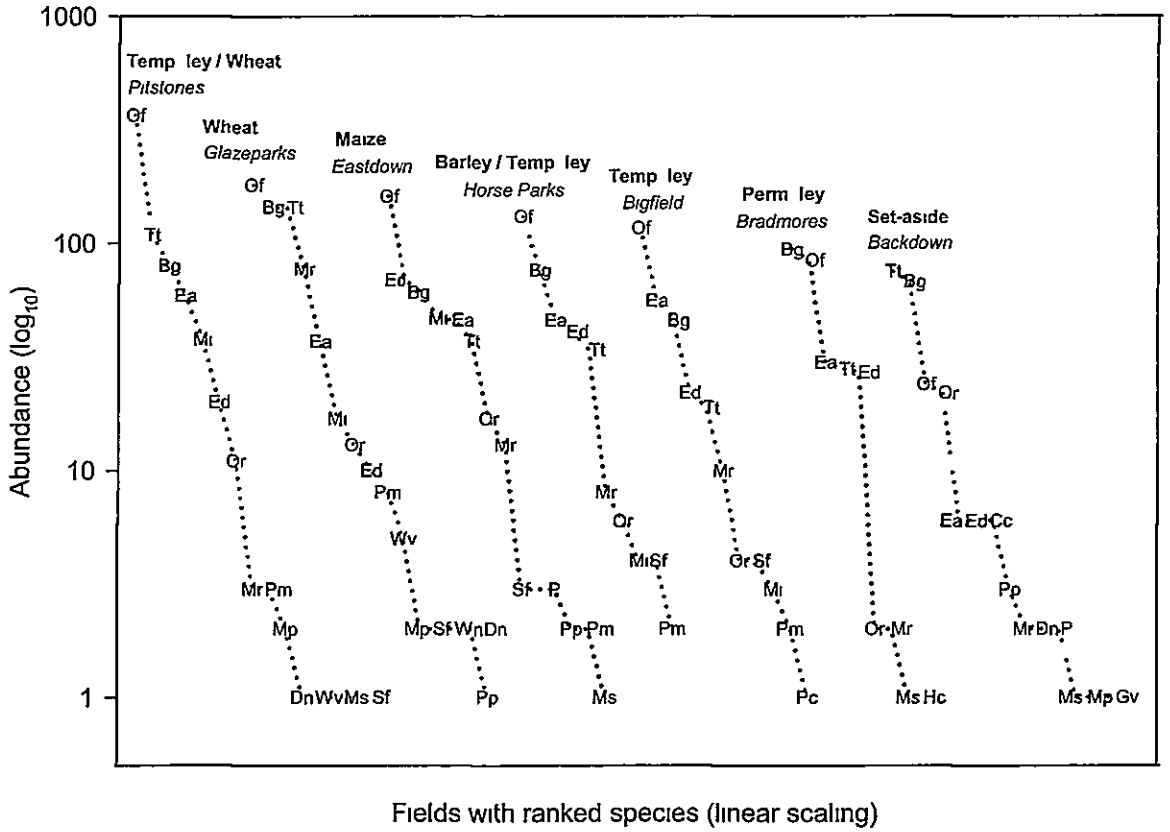

Figure 5-1 Ranked abundance plot (Whittaker plot) summarising composition and abundance of species for each field (see Table 5-2 for species names)

The highest number of species was recorded from Glazeparks and the lowest from Bradmores in permanent ley. Excluding set-aside, the number of species recorded in

each field correlated positively with the abundance of adults (R-sq = 0.84). In contrast Backdown in set-aside had a greater proportion of species relative to the total abundance of adults found there.

Variation in diversity between fields was evident. Backdown (Figure 5-2) was seen to have the highest value of α. Maize and wheat fields had higher diversity values than fields with barley, temporary and permanent ley. The lowest diversity was from the permanent ley field, Bradmores. In general, the pattern of diversity reflected that of the relative species richness between the fields.

The field with the highest dominance was the temporary ley /wheat field, Pitstones. Eastdown in maize had the lowest dominance and Glazeparks in wheat the second lowest although the difference between these values and the median value was not as pronounced.

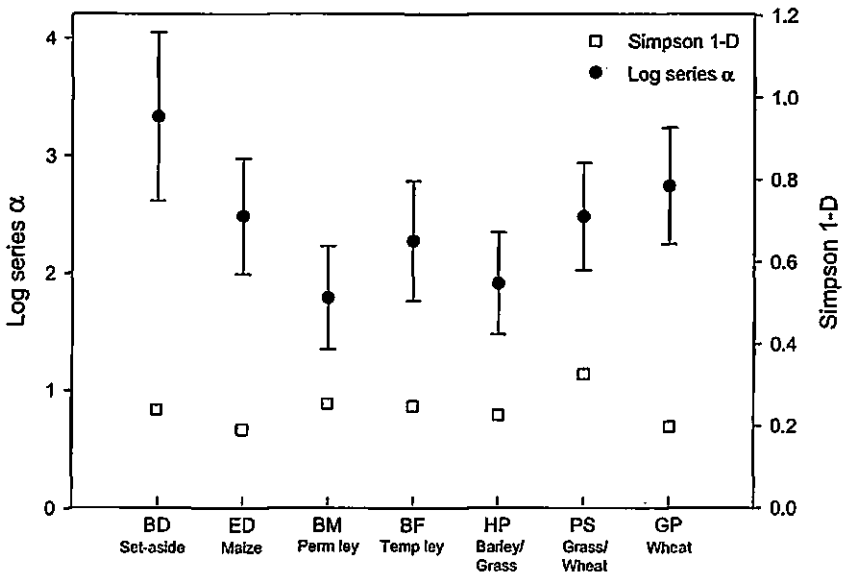

Figure 5-2. Log series α diversity index with 95% confidence limits and Simpson's index (1-D). The axis range for the Simpon index D is increased for clarity.

5.3.2 Seasonality of spider abundance over the time series: general observations

Broad seasonal variations in adult and immature ground densities are noted from all fields over the time series with higher densities in the summer and autumn months and lower densities in the winter and spring (Figure 5-3). Peaks in immature density were evident in most fields outside of the period between October 2001 and April 2002 when densities of both immatures and adults were low In 2001 immature densities peaked between early August and mid September In 2002 peaks were not so congruent - relatively small early peaks in immatures are seen between early May and mid June in the grass leys Bradmores and Bigfield, and Pitstones in wheat.

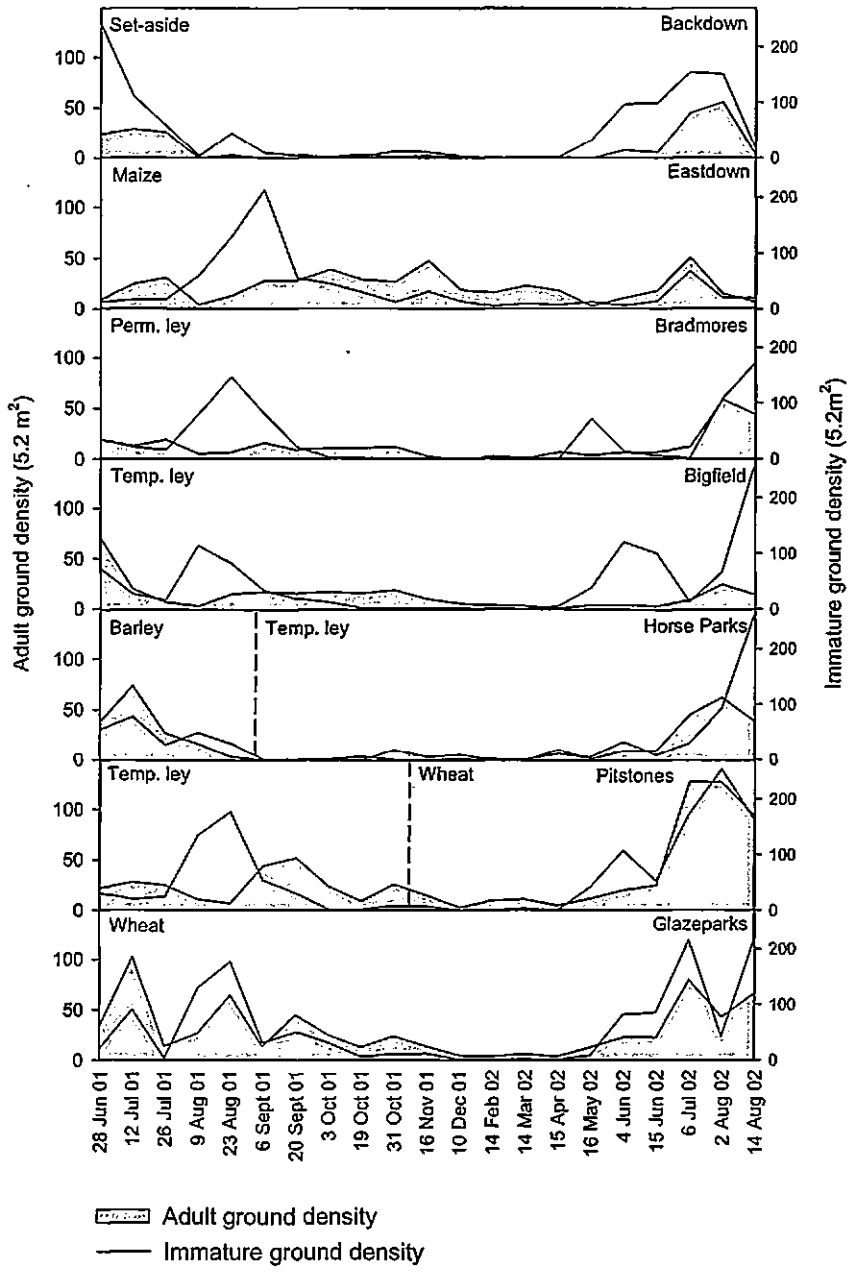

Figure 5-3. Ground densities of adult and immature linyphiids recorded between 28th June 2001 and 14th August 2002. Data following August are not included as comparable dates are not available for all fields.

Thereafter, densities increased in most fields and appeared to peak in early August in Pitstones with densities rising in Bradmores, Bigfield and Horse Parks beyond mid August. In Backdown, numbers decreased after the topping of set-aside. Only in

Bradmores in permanent ley did densities remain low after June although a short-lived decrease was observed in Glazeparks.

Adult densities showed less short-term variation than immatures For most fields, densities decreased from July to early August in 2001 with an earlier reduction in wheat Densities increased thereafter with relatively higher densities being recorded from wheat, Pitstones in temporary ley, and maize. After October, densities declined to relatively low levels the exception being maize where densities remained relatively high until ploughing in April. Adult densities increased again in mid May and more markedly from mid June. A peak in density was observed for most fields in early August. As for immatures high densities failed to develop in Bradmores with densities decreasing during July. A short-term decrease was observed also for adults in Glazeparks

In grass leys and maize in 2001, peaks in immatures densities occurred prior to increases seen in adults in August. For other fields modest correlations between adults and immatures where observed. Densities of *T tenuis* were seen to show a modest correlation with immatures in Pitstones in wheat (R-sq = 0 46) and *B gracilis* with immatures in Bradmores (R-sq = 0 57). Outliers were removed according to Grubb (1969) (cf. Sokal and Rohlf 1981) Comparing the overall abundance of all fields between years, a higher abundance of adults and immatures was recorded between July and August of 2002 than during the same period in 2001. Higher abundances were observed in 2002 in the rotated crops in Horse Parks (grass ley) and Pitstones (wheat) and also for all other fields relative to the previous year.

A similar pattern of adult to immature ratios is observed in all fields over the study period (Figure 5-4). Immatures predominate from August in 2001 diminishing in

percentage over the autumn until adults make up the greater part of the overwintering population. Immatures increase markedly again from April 2002 until May and June when the proportion of adults increase, the ratio shifting again to immatures after June.

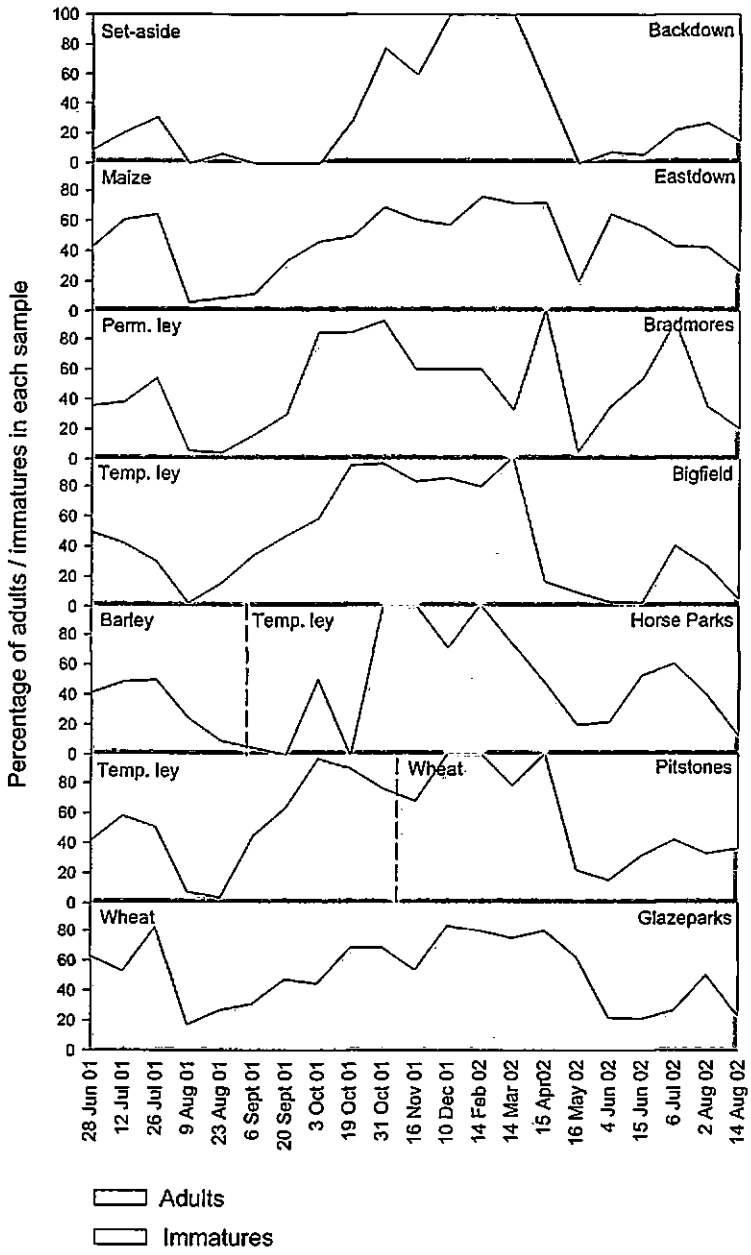

Figure 5-4. Relative percentages of adults and immatures in samples taken between 28th June 2001 and 14th August 2002. Data following August are not included as comparable dates are not available for all fields.

5.3.3 Exploratory data analysis

5.3.3.1 Correspondence Analysis

To determine whether a linear or unimodal analysis was more appropriate, beta diversity was estimated in accordance with the method described by Lepš and Šmilauer (2003) where Detrended Correspondence Analysis (DCA) is first performed to determine gradient lengths for each axis. As the greatest gradient length exceeded a value of 4 SD units (average standard deviation of species turnover) unimodal Correspondence Analysis was deemed most appropriate (relative to linearly derived Principal Component Analysis). A partial analysis (partially constrained) was conducted on all samples (n = 185), field and sampling date being included as covariables Crop types were added as nominal variables which were projected *post hoc* onto the ordination plot. Data were transformed by log(n+1) prior to analysis and samples with zero values for all species were removed A complication when using Chi-squared distance values is that species with low abundance may have a disproportionately large effect on the ordination - differences in samples containing several infrequently recorded species being over-emphasised A solution to this is to down-weight the rare species in proportion to their frequency. Although down-weighting was performed in CANOCO (see section *5 2 2.1 Exploratory techniques*) inter-site distances were still too great to show all the nominal variable centroids successfully whilst differentiating others. In view of this, species occurring in less than 10% of samples, with abundance in each sample equal or less than 2, were removed.

In CA, involution of the gradient ends can give rise to an arch shaped distortion when sites are considered similar owing to lack of presence of most species rather than the presence of members of the same species (Wartenberg, Ferson *et al* 1987) Although

used initially to determine gradient lengths, DCA was not performed for the final analysis as the detrending process did not visibly aid interpretation and has been found to give rise to aberrant results in some instances (Jackson and Somers 1991). Eigenvalues for principal axes 1 and 2 accounted for 41.9% (22.6% and 19.3% respectively) of the total variance (inertia) of species data (Table 5-3). From the biplot (Figure 5-5) of axes 1 and 2, set-aside is seen to clearly dissociate from other crops whilst permanent/temporary ley and maize/cereals respectively show some degree of association. The majority of centroids of species scores (being relative to species abundance) occur in the vicinity of cereals, maize and temporary ley, with *M. rurestris* and *O. retusus* showing the most separation from other species, both having particularly heterogeneous abundances between crops types. Substituting axis 2 for 3 (percentage variance 16.5%) gave a similar distribution of sites and species to the principal axes (not shown).

Table 5-3. Results of Correspondence Analysis on all samples (n =185) over the sampling period. Total inertia represents the total variation in species scores. Eigenvalues and the corresponding cumulative percentage variance of species data represent the proportion of the total inertia per axes shown.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.162	0.139	0.119	0.104	0.745
Species-environment correlations	0.455	0.406	0.105	0.369	
Cumulative percentage variance:-					
of species data	22.6	41.9	58.4	72.9	
of species-environment relation	41.9	70.5	72.2	89.9	
Sum of all eigenvalues					0.72
Sum of canonical eigenvalues					0.08

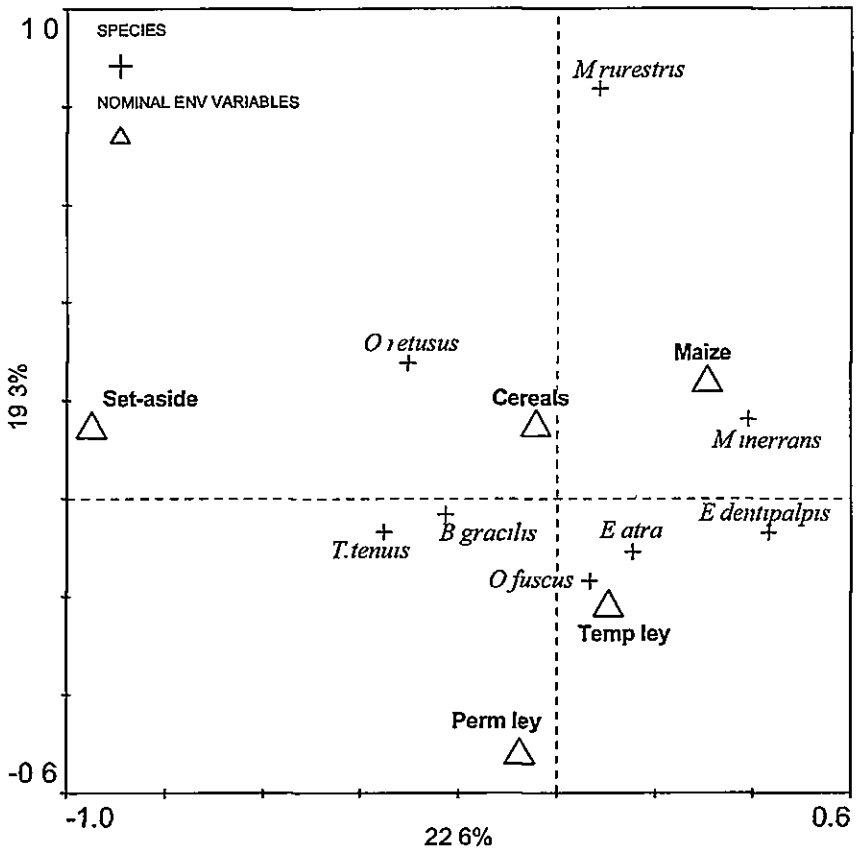

Figure 5-5 Biplot of Correspondence Analysis results with species scores and nominal environmental variables plotted to axis 1 (percentage variance 22 6%) and axis 2 (percentage variance 19 3%)

Species response curves give an illustration of the change in species abundance along a compositional gradient (Lepš and Šmilauer 2003) Response curves along the first ordination axis (Figure 5-6) were fitted using Generalised Additive Models (GAMs), available within CanoDraw.

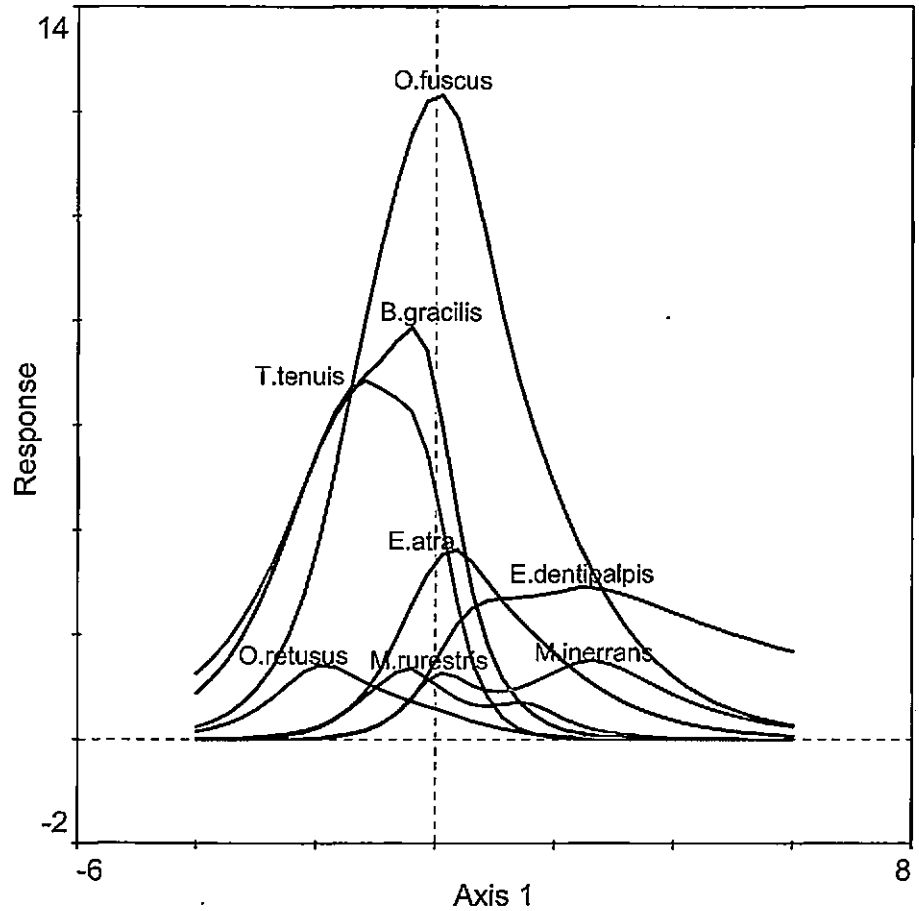

Figure 5-6. Response curves of seven species along axis 1 fitted using Generalised Additive Models.

A stepwise fitting procedure allowed for GAMs of increasing complexity (specified as degrees of freedom of the curve) to be fitted although as multiple species were compared, the fitted curves where smoothed by limiting to 3.5 DF (4.3 DF for *M. rurestris*). For the response variable, a poisson distribution appropriate to the count data was fitted. A strongly unimodal response curve is seen for *O. fuscus* which substantially overlaps those of other species. The response curves for *T. tenuis* and *B. gracilis* are similar to each other in shape and position with their optima being to the left of centre. *E.atra* and *E. dentipalpis* have lower curves and whilst *E. atra* has an obviously centralised optimum, the curve for *E. dentipalpis* is flattened and to the right of centre. *O. retusus* has a low shallow curve with a left biased optimum and both *M. inerrans* and *M. rurestris* display low bimodal curves.

5.3.4 Procrustes Analysis

Procrustes Analysis was used to compare assemblages in fields in 2001 and 2002 recorded over the congruent period between June and August Species abundance for each field consisted of the pooled abundance taken over the sampling period (sample sizes being equal). Principal Components Analysis (PCA) was selected as a suitable ordination method as gradient lengths using the pooled dataset were shorter than 4 SDs indicating relationships between variables to be approximately linear. Principal Component Analysis was carried out in CANOCO. Data were log transformed prior to analysis with scaling centred on sample distance. Procrustes analysis was performed on the principal axes of the PCA ordinations, cumulative percentage variance being 79 8% for both years.

The Procrustes analysis carried out using the PROTEST program (see section *5 2 2 1 Exploratory techniques*) generated the coordinates for the reference and the rotated configuration The associated m_{12} statistic (Table 2-1), based on the sum of the squared deviations, is an overall measure of goodness-of-fit of the configurations Values range between 0 and 1 with lower values being indicative of greater association. The significance of the m_{12} statistic is estimated using the permutation procedure in the PROTEST program whereby m_{12} values from large numbers of random configurations of the rotated matrix are related to the original fitted m_{12} to estimate the likelihood of the original value being derived by chance. A total of 9999 permutations plus the original configuration were run for significance testing

Table 5-4. Residual vectors for each field, residual SS and the goodness of fit measure, M_{12} with its associated p-value following Procrustes Analysis.

	Field	Residual
BD	Backdown	0.1416
ED	Eastdown	0.1236
BM	Bradmores	0.1299
BF	Bigfield	0.2742
HP	Horse Parks	0.2489
PS	Pitstones	0.5291
GP	Glazeparks	0.3510
Residual SS		0.5925
$M_{12} = 0.5048$		
P = 0.1504		

The p-value (Table 5-4) of the m_{12} statistic indicated that the association of the ordinations between years was not sufficiently concordant to be significant. Additionally, the graphical representation of the analysis (Figure 5-7) revealed little consistent structure although the length of the residual vector for Pitstones indicated that the assemblage had changed more than in the other fields.

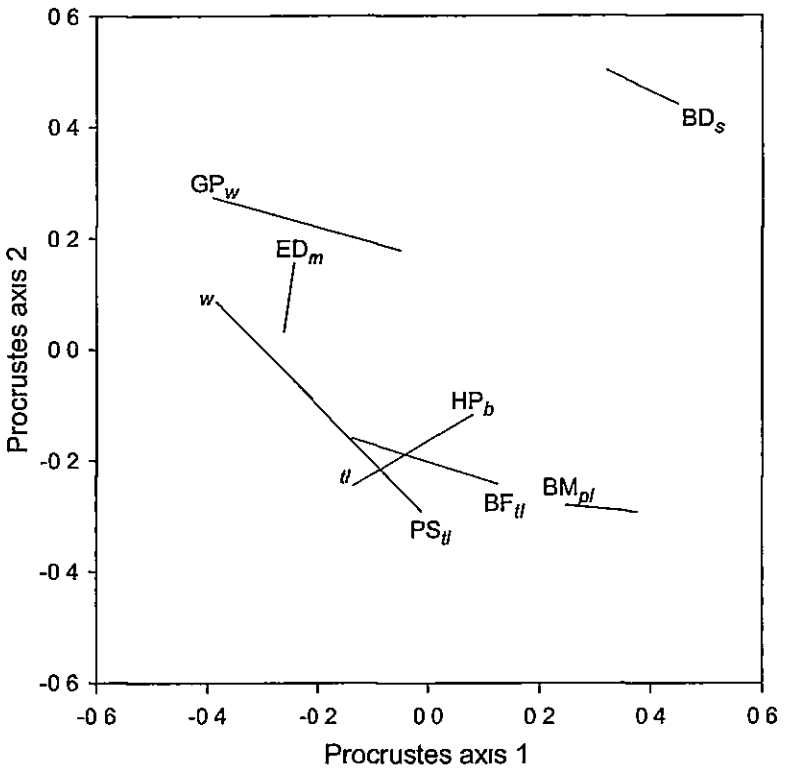

Figure 5-7 Procrustes analysis of PCA ordinations comparing fields in 2001and 2002 between June and August Lines represent residual vectors or the displacement of points (fields) between the reference (2001) and rotated (2002) configurations The position of the reference configuration in relation to the vectors is denoted by the placement of field abbreviation Field names are given in Table 5-4 Abbreviations for crop type are *s* – set-aside, *m* – maize, *pl* – permanent ley, *tl* – temporary ley, *b* – barley and *w* – wheat Where crop type differs between years the later crop type is abbreviated at the opposite end of the line to the field abbreviation

5.4 Discussion

As in other european-based studies (Bedford 1994; Kromp and Steinberger 1992; Nyffeler and Benz 1988; Toft 1989, Weyman, Jepson *et al* 1995), the data collected on this mixed-farm site confirmed that linyphiids are the dominant family found in fields under agricultural production Only the set-aside field Backdown was found to have a distinctly different assemblage to that of other fields. Although the field was designated only a year prior to data collection, the pasture was unimproved and grazed only sporadically owing to the field's relative isolation and higher elevation Spiders sampled here represented the families *Araneidae*, *Lycosidae*, *Tetragnathidae* and *Thomisidae* with the species *Pachygnatha degeeri* Sundevall, and *Xysticus cristatus* (Clerck) being

particularly abundant. Other studies have found semi-natural and natural grasslands not to be dominated by agrobiont spiders although they do share the same species (Duelli 1990; Samu and Szinetar 2002; Sunderland and Samu 2000). Compared to crops, the greater complexity of vegetation structure, a wider diversity of prey species, and the availability of suitable oviposition and overwintering sites could contribute to the higher abundance of non-linyphiids observed in set-aside. Reduced disturbance also enables species to persist which have univoltine life cycles with lengthier developmental phases. Non-linyphiid species also tend to be less dispersive at least in their adult phase when their larger size precludes aerial dispersal. Set-aside was the only field not to be dominated by *O.fuscus*, *T. tenuis* and *B. gracilis* being more abundant. Although these species are common agrobionts, the taller and more complex vegetation structure may be of benefit as *T. tenuis* tends to locate its web between 5 to 10 cm above ground level, supported by the surrounding vegetation (Sunderland 1996; Sunderland, Fraser *et al.* 1986a). Both *T. tenuis* and *B. gracilis* are also known to inhabit patches with greater vegetation structure (Alderweireldt 1994) and *T. tenuis* in particular is found to favour areas of tall, dense grass (Sunderland 1996) with semi-natural field margins being a particularly good source habitat for this species (Bell, Johnson *et al.* 2002).

There must however be some caution in suggesting that the conditions in set-aside disproportionately benefit epiphytic species compared to epigeic species. As discussed in Chapter 2 (*General materials and methods*), the sampling efficiency of the D-vac suction sampler is comparatively poor in the denser matrix of grass compared to the more open structure of wheat. The sward in Backdown was particularly dense and it is expected that sampling efficiencies were low in this field. That *T. tenuis* and *B. gracilis* both make webs higher in vegetation may result in these species being sampled with greater efficiency than epigeic species. Sunderland and Topping (1995) found both *T.*

tenuis and immatures to be sampled more efficiently by suction sampling owing to their presence in foliage. In set-aside the moderately high abundance and high proportion of immatures to adults compared with other fields might suggest that adult linyphiids were comparatively under-sampled. This may have also reflected on spider richness in Backdown and the α diversity value which was only marginally higher than for other fields. Of the two species found exclusively in set-aside, *G vivum* was a singleton and *C. concinna* numbered six.

Although α diversity values varied only moderately between fields, the distributions of rarer species between fields were not uniform, nor were rarer species especially 'clumped' in particular fields. It is probable that the sampling intensity was inadequate to show true species richness and instead the combined number of species, 21, is probably a closer representation of actual species richness, or, the number of species that could be expected to occur in any of the fields sampled All the less abundant species (<75 individuals) have widespread distributions and occur in a variety of habitats (Roberts 1993) and therefore may have a reasonable probability of being observed in any agricultural study given a sufficiently large sample size Of the typical agrobionts found, it is likely that no substantial portion of the indicative species remain undiscovered and if sampling was extended and intensified, other species found at low abundance could likely be 'tourist' or ubiquitous species Without a more intensive sampling protocol, it is difficult to separate those species which could be completing their lifecycles within fields from those which are casual dispersers from other habitats. This is especially true for set-aside which may be expected to have more distinct linyphiid species given the low degree of disturbance and emphasizes the need for knowledge of life-histories and habitat preferences to differentiate probable resident species

Oedothorax fuscus is seen to be the most abundant species sampled in the majority of fields on the farm including cereals. In other studies population densities in cereals estimated using suction sampling were found to be dominated by *M. rurestris*, *L. tenuis*, *B. gracilis* and *E. atra* (Sunderland and Topping 1993; Thomas and Jepson 1997; Thomas and Jepson 1999). Regional differences could account for this discrepancy in that in Southeast England, where these studies were conducted, a greater proportion of the land is under arable production compared to the pastoral/mixed farm systems of the Southwest. Climatic differences and associated changes in land use could be more or less favourable to certain linyphiid species. Thomas and Jepson (1997) found that the proportion of abundance in species shifted to dominance of *Oeothorax* spp. in heavily grazed pasture. De Keer and Maelfait (1988b) also remark that *O.fuscus*, unlike other species, tends to over-winter in pasture and is particularly suited to this habitat. The large proportion of the land under grass leys on the farm and in the surrounding landscape may be particularly beneficial to *O. fuscus*. Its high abundance in wheat could also be a result of its overall abundance in the environment even though the particular characteristics of the wheat crop (weed species, vegetation structure) and lack of disturbance from grazing animals are beneficial to epiphytic species such as *T. tenuis*.

Although evidence of life history patterns in the time series data are indirect (i.e. inferred through changes in density), the distinct peaks in immature abundance and high proportion relative to adults in May/June and August of both years (Figure 5-3, Figure 5-4) indicates a 'short summer, long winter' generation cycle observed in previous studies, especially for the *Erigone* and *Oedothorax* species (De Keer and Maelfait 1987a; De Keer and Maelfait 1988b). This pattern, which probably signifies emergence of immatures (Sunderland, Topping *et al.* 1996), is evident in the grass leys but not so clearly defined in other fields. In wheat, the greater overlap between generations may

occur owing to higher abundance and perhaps a corresponding spread of development rates Whether the greater volume of wheat compared to grass produces a more heterogeneous mix of temperatures and available food is not known though both affect development rates with temperature having the greater influence (De Keer and Maelfait 1987a) *T. tenuis* and *B. gracilis*, which occur in abundance in wheat, are also thought to have more complex life cycles with separate generations being less easily distinguished than other species (Sunderland, Topping *et al.* 1996)

In maize stubble in Eastdown, relatively large numbers of adults were sampled during the winter period which may be evidence of the low impact of the harvest in October and the lack of post-harvest operations before the following spring (see *Chapter 6*) Immatures too were relatively abundant though these are likely to have been later broods of the second generation for which low temperatures prevented further development. Although maize stubble appears to provide a suitable over-wintering site for some species, oviposition or emergence to some extent would have been negatively affected by ploughing in early May

In grass leys relatively high numbers of immatures were observed between March and May, earlier than in most fields (Figure 5-3), which could indicate that oviposition and emergence occurred earlier in leys owing to the presence of over-wintering spiders Adult densities however were lower than for the maize field although sampling efficiency could have been reduced in the denser matrix of the grass compared to the barer ground of the maize stubble. Sampling inefficiency could also could be exacerbated by migration into the lower stratum of the vegetation during cold periods (Schaefer 1977). A possible illustration of this can be seen in comparing the ground densities sampled by the D-vac (Figure 5-3) and G-vac (Figure 4-29) in the grass leys,

Bigfield and Horse Parks. Though both samplers recorded increasing denisities from June onwards, the highest density sampled in Horse Parks, using the G-vac, was between February and April, whilst using the D-vac this period had one of the lowest recorded densities in Bigfield. The value of grass leys as over-wintering refugia for spiders is not well documented as studies have tended to focus on natural and semi-natural sites which may be important for specific species such as *T. tenuis* (Bell, Johnson *et al.* 2002) and *Oedothorax apicatus* (Blackwall) (Lemke and Poehling 2002). *Oedothorax fuscus*, which is abundant in this study, is however noted to over-winter in pasture (De Keer and Maelfait 1988b). Although the value of grass leys as refugia was not confirmed in this study, a similar observation of the early appearance of large numbers of immatures was by noted by Thomas and Jepson (1997) who concluded that leys were an important source of potential colonisers of cereals.

Correlations between densities of *T. tenuis* and immatures were noted particularly in wheat fields. This could be an effect related to a patchy distribution of weeds in wheat which could result in a greater or lesser amount of the weedy areas being sampled on different occasions. As spiders are known to aggregate in weedier areas of the crop (Topping and Sunderland 1994), the higher sampling efficiency of epiphytic spiders may reflect this patchy distribution more than other species. Similarly, correlations between *B. gracilis* and immatures observed in permanent ley could relate to single species grazing which is seen to result in a more heterogeneous sward height (Downie, Ribera *et al.* 2000) both *B. gracilis* and immatures being sampled more efficiently in denser patches.

Correspondence analysis (Figure 5-5) revealed varying degrees of separation between crop types with abundant species in particular showing dispersion along the x-axis

(Figure 5-6) A possible explanation for the distribution of species along this axis could be that it defines a gradient of structural complexity Higher abundance of the epiphytic species *T tenuis* and *B. gracilis* occur in the more diverse set-aside and cereals and lower abundance in the less complex temporary ley and maize. It might be noted that maize was comparatively weed free in both years although this is a difficult crop to quantify in structural terms as spider abundance probably relates more to weed density than to the crop itself The response curves for the *Erigone* species indicate an opposing trend with lower abundances in set-aside and higher abundances in temporary ley and maize. The pattern observed here does agree to an extent with a study modelling populations of *Erigone* spp across agricultural gradients where *E dentipalpis* associated more with low intensity grassland than with Autumn sown cereals and *E. atra* was negatively associated with plant species richness (Downie, Ribera *et al.* 2000). A similar relationship has also been observed for *E atra* occurring in grass plots with differing numbers of plant species (Edwards, Butler *et al* 1975) Without explanatory variables the interpretation of indirect gradient analysis is however speculative although the results are potentially useful as preliminary data which can assist in formulating hypotheses for further study.

The results of the correspondence analysis suggest though that although common agrobiont species do occur in all agricultural crops, there is evidence of a non-uniform distribution The Procrustes analysis however indicated that linyphiid assemblages in crops were not consistent between years although when temporary ley is rotated with wheat, the agrobiont linyphiid assemblage changes to a greater extent than when the same crop is grown in successive years

As previously discussed in relation to maize, a structurally dependent response may not be directly associated with the crop but could be instead related to the weed species the crop supports. Thus, if abundance of linyphiids were sensitive to vegetation structure a weedy crop of maize could have a similar assemblage to a weedy crop of wheat. In this respect the management of the crop plays an important role in determining the field environment. Smith *et al.* (2008) have shown that management regimes in certain crops select for crop-specific assemblages of weeds which are themselves associated with specific assemblages of invertebrates. Spiders as generalist predators would perhaps not be as intimately associated with weed species as some primary consumers, however differences in the physiognomy of the dominant weed species between crops may produce consistently observed assemblage differences.

5.4.1 Further work

Assigning samples to a nominal classification of 'crop type' is problematic as this may not be the most important determiner for the assemblage found there. A variety of factors both present and historical could have specific effects on the species assemblage.

An extension to the work presented here would be to measure a number of relevant environmental variables (e.g. weed cover, plant species diversity, bare ground, litter cover, canopy height, grazing intensity, sowing date etc) which could be important in determining species composition. The relationship of these variables to the observed data can then be analysed using direct gradient analysis methods such as the unimodal Canonical Correspondence Analysis or the linear method of Redundancy Analysis. The significance of the regression of important environmental variables and the response

variable can be determined using the Monte Carlo permutation test which is applicable to ordination analyses where a distribution dependent test statistic is not known *a priori*.

The original data collection exercise which required a small number of sites to be sampled over time, presents statistical problems when comparing repeated samples taken between fields In this situation, samples, not sites, are replicated and samples do not satisfy the required condition of independence (i.e. they are pseudoreplicated) A further study to investigate the spider assemblage in different crops would require a fully replicated design with crop type being replicated at the treatment level. If the investigation was compared at field scale as a 'natural experiment', comparing crop types across existing environmental gradients (e g. soil type, latitude, elevation etc) could be considered Alternatively if certain variables were thought to be important (e g. tillage method, herbicide treatment), a manipulation experiment could be conducted in smaller plots with treatments being replicated in a randomised complete block design, or a factorial or split plot design if interaction effects were to be considered In these situations data could also be analysed using multivariate regression methods

With regards to determining species richness in dense vegetation, as was the case for sampling in set-aside, pitfall trapping is more effective at sampling epigeic species and also nocturnally active species than suction sampling (Dinter 1995). Although limited regarding estimating actual densities and relative species abundance, the continuous sampling of ground-level fauna makes this technique useful if used in conjunction with other methods, especially when detailed knowledge of species richness is required. Sunderland and Topping (1987) describe a method for accurate density estimation of invertebrates involving a succession of measures applied to the sample area, these being suction sampling, removal and searching of vegetation, surface searching and finally

pitfall trapping for seven days. Although a simpler and quicker method using suction sampling and destructively surface searching is also advocated (Sunderland and Topping 1995), such measures are labour intensive and time consuming and are unsuitable for extensive studies. For estimating species richness in a natural calcareous grassland Standen (2000) found that sufficient overlap occurred between epigeic and epiphytic species, that either suction sampling or pitfall trapping was adequate. Suction sampling alone could then be sufficient if enough sampling is undertaken, however, without prior knowledge of the proposed site, the decision of how much sampling is sufficient is difficult and a more intensive sampling regime may be prudent especially when the site is perceived to be diverse (Scharff, Coddington *et al.* 2003).

5.4.2 Conclusions

The linyphiid assemblages sampled in this study were similar to those of arable and ley fields sampled in other UK and north european studies. Although the dataset was limited with respect to the absence of environmental variables, the results broadly support findings from previous studies.

A summary of the findings are as follows:-

- Typical agrobiont linyphiid species dominated grass leys, cereals and maize
- Set-aside supported higher numbers of non-linyphiid spiders than fields under agricultural production (livestock grazing, arable)
- Maize stubble supported relatively high abundance of over-wintering spiders

- Early emergence of immatures from grass leys indicated that they may be important overwintering refugia for some species and may constitute important sources for recolonising crops in spring.
- Assemblages of agrobiont linyphiids may differ between crops type; related management and the weed/crop vegetation structure being possible determinants.
- Use of suction sampling alone may be insufficient to provide estimates of species richness owing to sampling inefficiency in dense swards and the sampling intensity applied

Chapter 6. Effect of field operations on spider populations

6.1 Introduction

Previous studies have found spider populations to be reduced by farming operations and practice (Thomas and Jepson 1997; Thorbek and Bilde 2004). The greater part of this reduction is likely through the direct physical disturbance and abrasion from the operation (Wardle 1995), and the sudden exposure to new or immoderate environmental conditions which increase mortality or dispersal from the disturbed area. The objective of this study is to determine whether farming operations occurring over the annual cropping cycle have differential effects on the populations of linyphiid spiders in grass, maize, wheat and barley.

6.2 Materials and methods

6.2.1 For site description and sample methodology see Chapter 2.

6.2.2 Data analysis

Densities of adult and immature linyphiids sampled prior to farming operations were compared to post-operation densities sampled over subsequent weeks. For the majority of operations considered, the post-operation sampling period was between 1 and 2 months although in some instances this was either extended to include associated operations or shortened when densities became very low. The data used here represents samples collected for the monitoring of field populations (*Chapter 5*) which were

supplemented as required with additional sampling dates before and after field operations.

For the repeated measures analysis, a number of two-sample Wilcoxon rank sum tests (Sokal and Rohlf 1981) were used to compare the density prior to harvest with densities sampled after harvest. Lack of replication owing to the unavailability of fields with concurrent farming operations meant a more robust analysis could not be performed. The number of tests performed here may also increase the possibility of Type I errors. Bonferroni correction however may result in increasing the probability of Type II errors (Nakagawa 2004). In view of these limitations, the results presented must be viewed conservatively and in context with results from other relevant studies

6.3 Results

6.3.1 Backdown – set-aside

6.3.1.1 Adults and immatures

Following the 2001 topping operation (Figure 6-1), significant reductions in density were observed for adults (Ratio = 0, P = 0.0044, W = 56 5) and immatures (Ratio = 0 05, P = 0 0054, W = 21). An increase to near pre-operation densities was observed for immatures 17 days after topping on 23rd August (Figure 6-1). Density of immatures declined thereafter to near zero levels by 3rd October. No recovery was observed for adults following the topping operation and very low densities were recorded thereafter

The extended period between pre- and post-topping samples in 2002 (Figure 6-1), prevents direct comparison with the previous year over the short term. Prior to the topping operation the density of adults and immatures was lower compared to the

previous year. A significant increase (Ratio = 5.67, P = 0.0038, W = 21) (Figure 6-1) in adult density was observed although immatures showed no significant change from pre-operation densities.

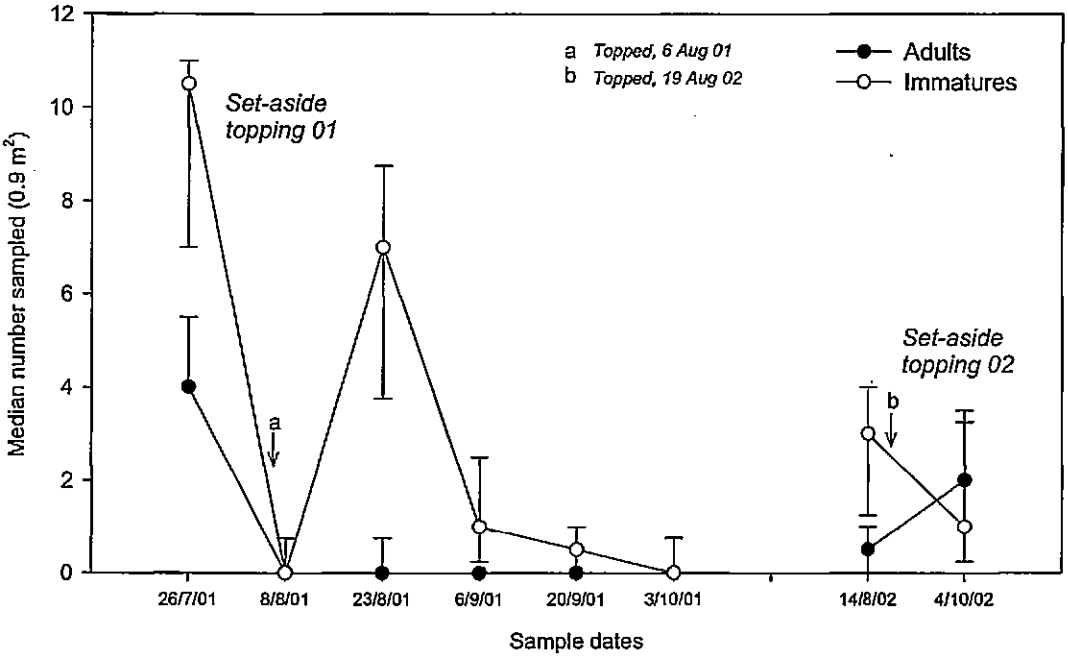

Figure 6-1. Median densities of linyphiids (adults, immatures) sampled before and after topping in Backdown (set-aside) in 2001 and 2002. Median = symbol, first quartile = lower bar, third quartile = upper bar.

Table 6-1. Mann-Whitney analysis of densities of adult and immature linyphiids sampled before and after topping in Backdown (set-aside) in 2001 and 2002. Asterisks indicates significance level. 'NS' indicates analyses which are not significant. The ratio of post-operation to pre-operation density is shown to indicate the direction of change where a value <1 is a reduction, a value >1 is an increase and 1 indicates no change.

Crop	Dates	Operation	Adults sig. rel. to pre. op.	Ratio rel. to pre. op.	Imm's sig. rel. to pre. op.	Ratio rel. to pre. op.
Set-aside	26/7/01	Pre topping				
	9/8/01	Post topping	**	0	**	0.05
	23/8/01	Post topping	*	0.12	NS	0.76
	6/9/01	Post topping	**	0	*	0.16
	20/9/01	Post topping	**	0	**	0.07
	3/10/01	Post topping	**	0	**	0.05
	14/8/02	Pre topping				
	4/10/02	Post topping	**	5.67	NS	0.65

* = p < 0.05, ** = p < 0.01, *** = p < 0.001, NS = not significant

6.3.1.2 Species

Species present prior to topping on 6th August 2001 all showed marked reductions to the extent that no adult linyphiids were recorded in the post-operation sample Significant declines were observed for *O retusus* (P = 0 0239, W = 52 5) and *T tenuis* (P = 0 0289, W = 52) and the decline of *B gracilis* was close to significant (P = 0 0729, W = 49 5).

6.3.2 Eastdown - maize

6.3.2.1 Adults and immatures

No significant change in the density of adults and immatures was observed immediately following maize harvest on 3rd October 2001 (Figure 6-2) Densities recorded 16 days after harvesting were not significantly different to pre-operation densities (Table 6-2).

Relatively low densities were recorded for adults and immatures prior to ploughing in April. A declining trend was observed over the period of ploughing and flat-rolling operations although densities did not reduce significantly after each operation.

Density of adults and immatures recorded 7 days following the maize harvest on 7th October 2002 (Figure 6-2) were not significantly reduced compared to pre-harvest density (Table 6-2).

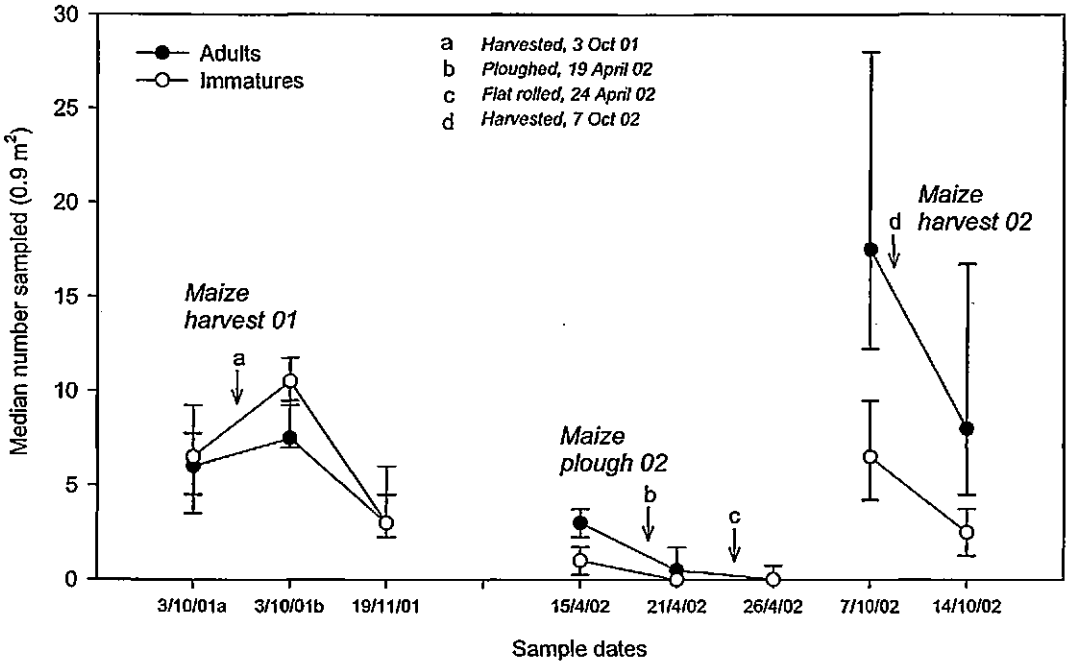

Figure 6-2. Median densities of linyphiids (adults, immatures) sampled before and after field operations in Eastdown (maize) in 2001 and 2002. Median = symbol, first quartile = lower bar, third quartile = upper bar.

Table 6-2. Mann-Whitney analysis of densities of adult and immature linyphiids sampled before and after field operations in Eastdown (maize) in 2001 and 2002. Asterisks indicates significance level. 'NS' indicates analyses which are not significant. The ratio of post-operation to pre-operation density is shown to indicate the direction of change where a value <1 is a reduction, a value >1 is an increase and 1 indicates no change.

Crop	Dates	Operation	Adults sig. rel. to pre. op.	Ratio rel. to pre. op.	Imm's sig. rel. to pre. op.	Ratio rel. to pre. op.
Maize	3/10/01(a)	Pre harvest				
	3/10/01(b)	Post harvest	NS	1.18	NS	1.47
	19/10/01	Post harvest	NS	0.74	NS	0.64
	15/4/02	Pre plough				
	21/4/02	Post plough	NS	0.44	NS	0.14
	26/4/02	Post plough	*	0.22	NS	0.14
Maize	7/10/02	Pre harvest				
	14/10/02	Post harvest	NS	0.57	NS	0.49

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, NS = not significant

6.3.2.2 Species

No significant change in the density of individual species was observed immediately following the maize harvest in October 2001. Species densities also did not differ significantly in the sample taken 16 days after harvesting

Prior to ploughing in April 2002, relatively low densities were recorded for all species. Following ploughing a significant reduction was observed only for *E dentipalpis* (Ratio 0.2, P = 0.0341, W = 51) No significant differences in species density were recorded following the maize harvest in October 2002

6.3.3 Pitstones – grass / wheat

6.3.3.1 Adults and immatures

In 2001, 10 days following the ploughing of the grass ley on 22nd October, (Figure 6-3) adult density was seen to have increased significantly (Ratio 2.89, P = 0 0066, W = 22) (Table 6-3) although from a low pre-operation density. A declining trend to very low densities was then observed in both adults and immatures from 1st November to 10th December.

Immatures recorded in wheat at relatively high density on 28th August 2002, (Figure 6-3) showed a significant and marked reduction (Ratio = 0 09, P = 0.0049, W = 57) (Table 6-3) 13 days following harvesting. A significant reduction was also observed for adults (Ratio 0 06, P = 0 0044, W = 57).

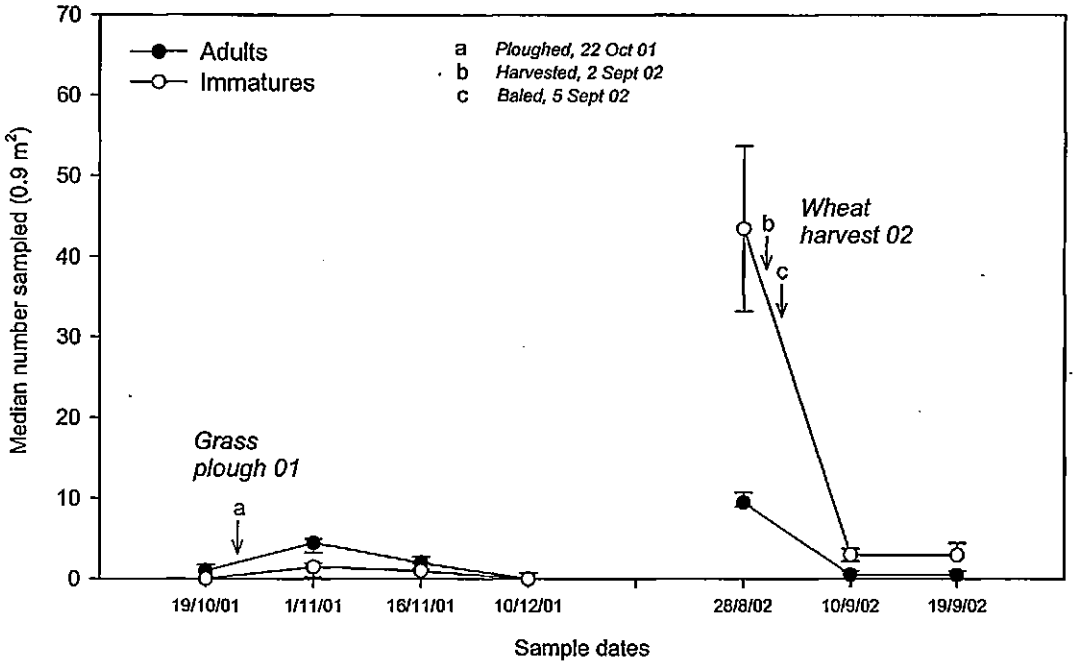

Figure 6-3. Median densities of linyphiids (adults, immatures) sampled before and after field operations in Pitstones (grass / wheat) in 2001 and 2002. Median = symbol, first quartile = lower bar, third quartile = upper bar.

Table 6-3. Mann-Whitney analysis of densities of adult and immature linyphiids sampled before and after field operations in Pitstones (grass / wheat) in 2001 and 2002. Asterisks indicates significance level. 'NS' indicates analyses which are not significant. The ratio of post-operation to pre-operation density is shown to indicate the direction of change where a value <1 is a reduction, a value >1 is an increase and 1 indicates no change.

Crop	Dates	Operation	Adults sig. rel. to pre. op.	Ratio rel. to pre. op.	Imm's sig. rel. to pre. op.	Ratio rel. to pre. op.
Grass	19/10/01	Pre plough				
	1/11/01	Post plough	**	2.89	NS	8
	16/11/01	Post plough	NS	1.67	NS	7
	10/12/01	Post plough	NS	0.33	NS	0
Wheat	28/8/02	Pre harvest				
	10/9/02	Post harvest	**	0.06	**	0.09
	19/9/02	Post harvest	**	0.05	**	0.08

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, NS = not significant

6.3.3.2 Species

Relatively low densities were recorded for all species on 19th September prior to ploughing of the grass ley in 2001. No significant changes in density were recorded for individual species following ploughing although the presence of *E dentipalpis* was recorded only from the post-operation sample.

Following the 2002 wheat harvest, significant declines were observed in species displaying the largest pre-harvest densities, these being *B gracilis* (Ratio = 0.11, P = 0 0039, W = 57), *T. tenuis* (Ratio = 0, P = 0.0057, W = 56) and *O fuscus* (Ratio = 0, P = 0.0031, W = 57) No significant change in density was observed for other species.

6.3.4 Horseparks – barley / grass

6.3.4.1 Adults and immatures

Harvesting occurred intermittently over a 7 day period allowing for further sampling of the area where the crop remained. In a sample taken in the unharvested area on 6th August, adult linyphiids were significantly lower in density (P = 0.0171, W = 54) than that recorded prior to harvesting on 26th July.

No significant change in adult and immature density was observed in the harvested area three days following the partial harvest on 3rd August (Figure 6-4) (Table 6-4). By 9th August adult density had declined significantly (Ratio = 0.04, P = 0 0045, W = 56.5) to a near-zero level although density of immatures was not significantly different to that recorded prior to harvesting.

Following ploughing, harrowing and flat-rolling operations, adult linyphiids remained at near-zero densities. Although density of immatures did not show any significant change following ploughing, no immatures were recorded in the sample taken after harrowing and flat-rolling operations (Ratio = 0, P = 0.0159, W = 53.5).

A significant decline in adult linyphiids (Ratio = 0.08, P = 0.0156, W = 53.5) was recorded six days following the grass harvest in 2002 (Figure 6-4). In the following sample, immatures recorded at low density prior to harvest, increased significantly (Ratio = 32, P = 0.0099, W = 23) whereas adult density did not differ significantly from that observed prior to harvesting.

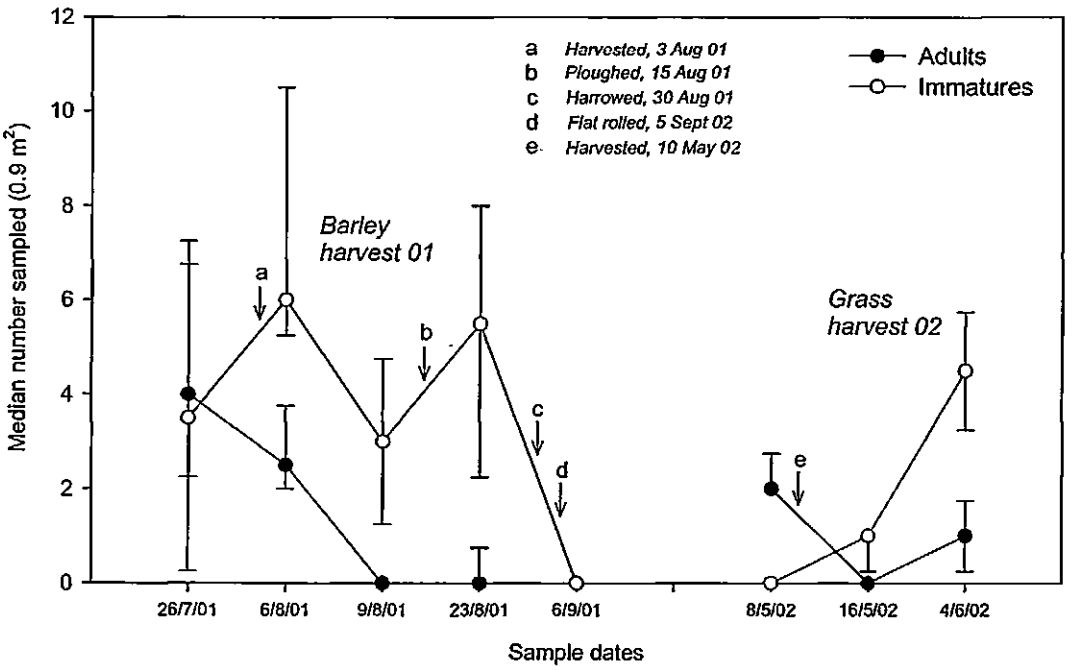

Figure 6-4. Median densities of linyphiids (adults, immatures) sampled before and after field operations in Horse Parks (barley / grass) in 2001 and 2002. Median = symbol, first quartile = lower bar, third quartile = upper bar.

Table 6-4 Mann-Whitney analysis of densities of adult and immature linyphiids sampled before and after field operations in Horse Parks (barley / grass) in 2001 and 2002. Asterisks indicates significance level 'NS' indicates analyses which are not significant The ratio of post-operation to pre-operation density is shown to indicate the direction of change where a value <1 is a reduction, a value >1 is an increase and 1 indicates no change

Crop	Dates	Operation	Adults sig. rel to pre op	Ratio rel to pre op	Imm's sig rel to pre op	Ratio rel to pre op
Barley	26/7/01	Pre harvest				
	6/8/01	Post harvest	NS	0 59	NS	1 81
	9/8/01	Post harvest	**	0 04	NS	0 67
	9/8/01	Pre plough				
	23/8/01	Post plough	NS	3	NS	1 61
	6/9/01	Post plough	NS	0	**	0
Grass	8/5/02	Pre harvest				
	16/5/02	Post harvest	*	0 08	NS	4
	4/6/02	Post harvest	NS	0 75	**	32
* = p < 0 05, ** = p < 0 01, *** = p < 0 001, NS = not significant						

6.3.4.2 Species

Densities of all species recorded prior to harvesting and ploughing were relatively low and no significant change in density was observed for any species following either operation. Relatively low densities of adults were recorded prior to the grass harvest in 2002 Many species were absent from the post-harvest sample though no significant change in density was observed

6.3.5 Bigfield – grass

6.3.5.1 Adults and immatures

A significant reduction in the density of adult and immature linyphiids (Ratio = 0.23, P = 0.0073, W = 56 and Ratio = 0 49, P = 0 0235, W = 53.5 respectively) was observed in samples taken the day following the second grass harvest of 2001 on 1st June. (Figure 6-5 and Table 6-5). Adult density remained at a similar low level thereafter although on

9th August immatures were seen to have increased to a density similar to that recorded prior to harvesting.

Low densities of adults and immatures were observed prior to the first grass harvest on 10th May 2002 (Figure 6-5 and Table 6-5). Following harvesting, adult density remained low and similar to pre-harvest levels. Immature density however increased significantly in the two samples taken at 6 days and 25 days following harvesting (Ratio = 38, P = 0.0036, W = 21 and Ratio = 120, P = 0.0037, W = 21 respectively).

Adult density decreased significantly (Ratio = 0.17, P = 0.0047, W = 57) (Table 6-5) 8 days following the second grass harvest on 28th June 2002. Immatures recorded at low density prior to harvesting showed no significant change. Immature density increased significantly in the following sample (P = 0.0036, W = 21) and although an increase in adult density was observed this was still significantly below that recorded prior to harvesting (Ratio = 0.46, P = 0.0338, W = 52.5).

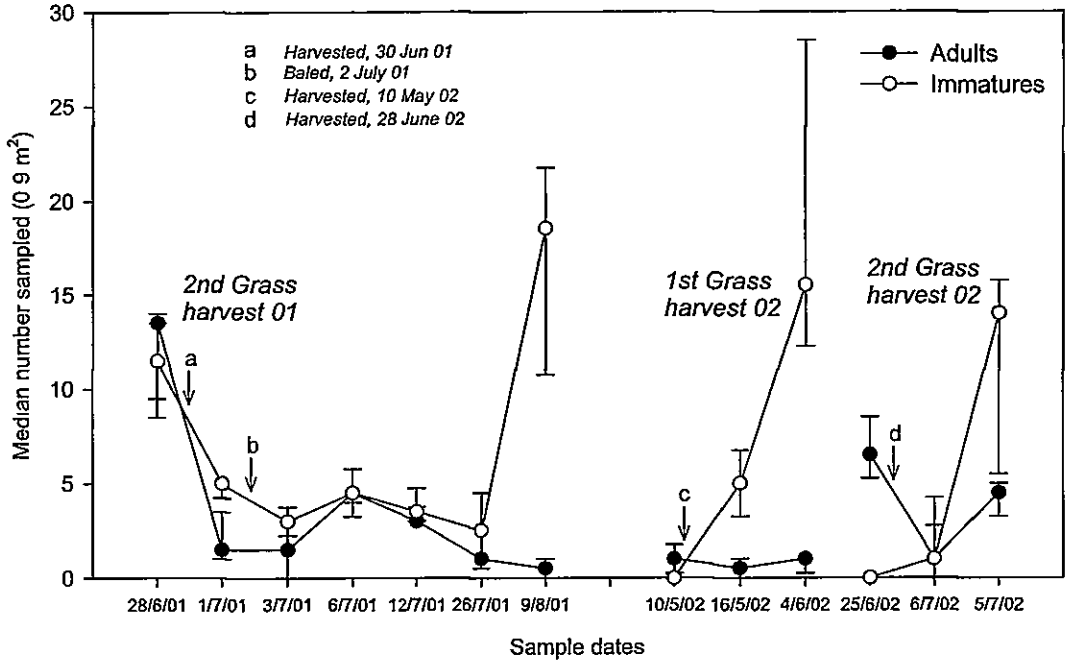

Figure 6-5 Median densities of linyphiids (adults, immatures) sampled before and after field operations in Bigfield (grass) in 2001 and 2002 Median = symbol, first quartile = lower bar, third quartile = upper bar

Table 6-5 Mann-Whitney analysis of densities of adult and immature linyphiids sampled before and after field operations in Bigfield (grass) in 2001 and 2002 Asterisks indicates significance level 'NS' indicates analyses which are not significant The ratio of post-operation to pre-operation density is shown to indicate the direction of change where a value <1 is a reduction, a value >1 is an increase and 1 indicates no change.

Crop	Dates	Operation	Adults sig rel to pre op	Ratio rel to pre op	Imm's sig rel to pre op	Ratio rel to pre op
Grass	28/6/01	Pre harvest				
	1/7/01	Post harvest	**	0 23	*	0 49
	3/7/01	Post harvest	**	0.15	**	0 25
	6/7/01	Post harvest	**	0 39	*	0 4
	12/7/01	Post harvest	**	0 28	**	0 37
	26/7/01	Post harvest	**	0.1	**	0 22
	9/8/01	Post harvest	**	0 04	NS	1 58
	10/5/02	Pre harvest				
	16/5/02	Post harvest	NS	0 57	**	38
	4/6/02	Post harvest	NS	0 57	**	120
	25/6/02	Pre harvest				
	6/7/02	Post harvest	**	0 17	NS	n/a
	5/8/02	Post harvest	*	0 46	**	n/a

* = p < 0 05, ** = p < 0 01, *** = p < 0 001, NS = not significant

6.3.5.2 Species

Following the second grass harvest in 2001, a significant decline in density was observed for *E. atra* (P = 0.023, W = 53.5) and *B. gracilis* (P = 0.0056, W = 56). Species were present at low density prior to the first harvest in 2002 and following harvesting, *E. atra, O. fuscus* and *T. tenuis* were not recorded. Following the second grass harvest in 2002, a significant reduction in density was observed for *B. gracilis* (P = 0.0044, W = 56.5) with *T. tenuis* close to significance (P = 0.0729, W = 49.5).

6.3.6 Glazeparks – wheat

6.3.6.1 Adults and immatures

The wheat crop in Glazeparks was partially harvested on 23rd July and completed on 28th August. Samples were taken in both harvested and unharvested areas of the field, up to and including samples taken prior to ploughing on 19th September.

A decline in linyphiid density was recorded 1 day and 3 days following the partial harvest on 23rd July (Figure 6-6). The decline was significant for immatures on the 24th (Ratio = 0.37, P = 0.0074, W = 56) and significant for both immatures (Ratio = 0.06, P = 0.0043, W = 57) and adults (Ratio = 0.25, P = 0.0051, W = 57) on the 26th (Table 6-6). On 9th August, immature densities were observed to have recovered to pre-harvest levels. Little variation in density was observed between 9th and 19th August although densities showed a declining trend following ploughing on 26th September with a significant reduction observed following cultivation on 9th October (Ratio = 0.12, P = 0.0095, W = 55.5).

Recovery in adult density occurred later than for immatures with a density similar to that recorded pre-harvest observed by 19th September A declining trend in density was observed after ploughing and cultivation operations with a significant reduction occurring following cultivation (Ratio = 0.29, P = 0.0073, W = 56).

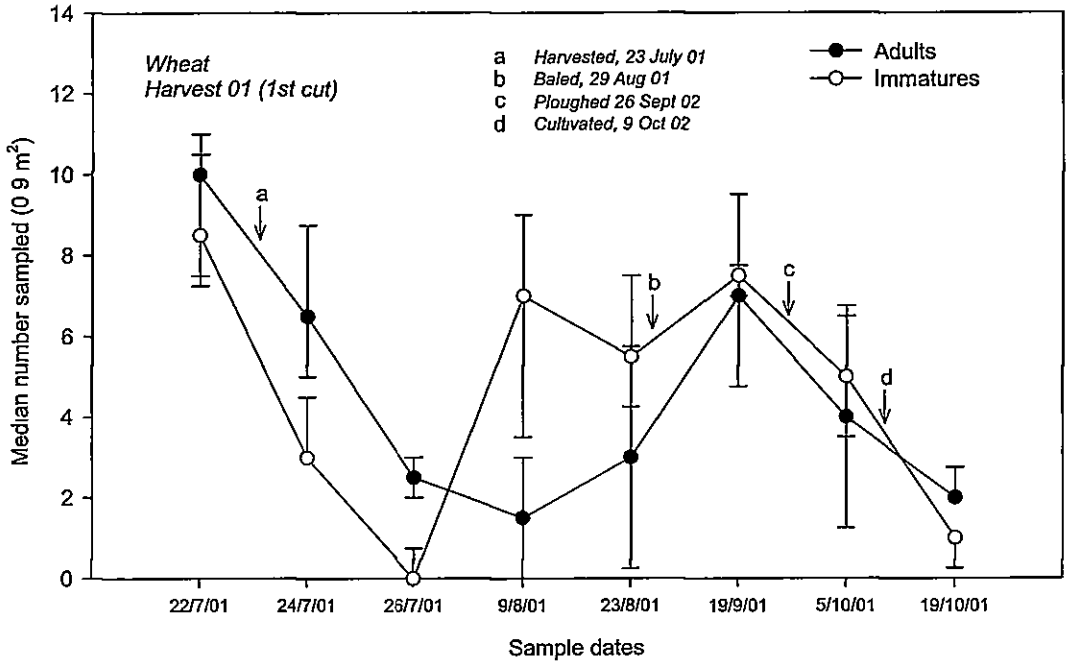

Figure 6-6 Median densities of linyphiids (adults, immatures) sampled before and after field operations (1st cut) in Glazeparks (wheat) in 2001 Median = symbol, first quartile = lower bar, third quartile = upper bar.

Table 6-6 Mann-Whitney analysis of densities of adult and immature linyphiids sampled before and after field operations in Glazeparks (wheat) in 2001. Asterisks indicates significance level 'NS' indicates analyses which are not significant The ratio of post-operation to pre-operation density is shown to indicate the direction of change where a value <1 is a reduction, a value >1 is an increase and 1 indicates no change

Crop	Dates	Operation	Adults sig rel to pre op	Ratio rel to pre op	Imm's sig rel to pre op	Ratio rel to pre op
Wheat	22/7/01	Pre harvest				
	24/7/01	Post harvest	NS	0.74	**	0.37
	26/7/01	Post harvest	**	0 25	**	0.06
	9/8/01	Post harvest	**	0.19	NS	0.75
	23/8/01	Post harvest	**	0 33	NS	0.75
	19/9/01	Post harvest	NS	0 79	NS	0.96
	19/9/01	Pre plough				
	5/10/01	Post plough	NS	0 56	NS	0 62
	19/10/01	Post plough	**	0 29	**	0 12
* = p < 0 05, ** = p < 0 01, *** = p < 0 001, NS = not significant						

In the remaining unharvested area of the field (Figure 6-7), immatures increased in density between 22nd July and 23rd August (Table 6-7). No significant change in density was recorded 2 days following harvesting on 30th August although a significant decline was noted after 9 days (P = 0.0048, W = 57) on 6th September. Density of immatures did not significant change on 19th September and thereafter sampling reverted to include the whole field (Figure 6-6). Densities of adults in the remaining unharvested area were variable prior to harvesting. Following harvesting a significant reduction (P = 0.0121, W = 55) was observed after 2 days on 28th August and densities remained at a similar level thereafter.

Following the wheat harvest on 2nd September 2002 (Figure 6-7), a significant reduction in density was observed after 8 days for adults (Ratio = 0.15, P = 0.0082, W = 56) and immatures (Ratio = 0.11, P = 0.0047, W = 57) (Table 6-7). From 10th September to 18th October densities of adults and immatures remained significantly below that recorded prior to harvest.

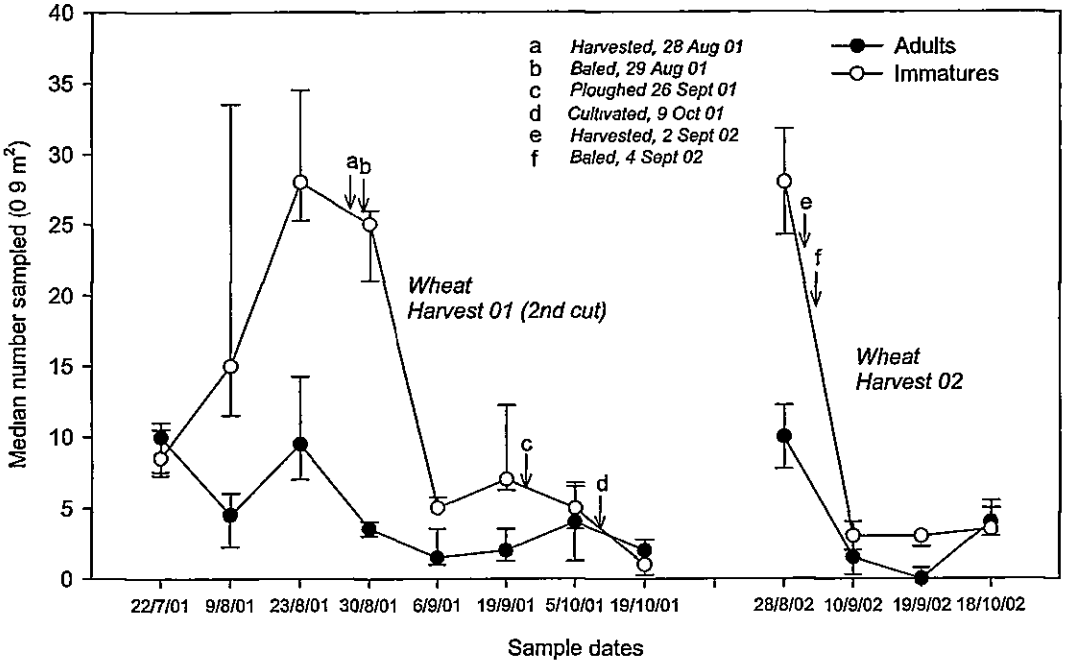

Figure 6-7 Median densities of linyphiids (adults, immatures) sampled before and after field operations (2nd cut) in Glazeparks (wheat) in 2001 Median = symbol, first quartile = lower bar, third quartile = upper bar

Table 6-7 Mann-Whitney analysis of densities of adult and immature linyphiids sampled before and after field operations in Glazeparks (wheat) in 2001 and 2002 Asterisks indicates significance level 'NS' indicates analyses which are not significant The ratio of post-operation to pre-operation density is shown to indicate the direction of change where a value <1 is a reduction, a value >1 is an increase and 1 indicates no change

Crop	Dates	Operation	Adults sig rel to pre op	Ratio rel to pre op	Imm's sig rel to pre op	Ratio rel to pre op
Wheat	22/7/01	Pre harvest				
	9/8/01	Pre harvest				
	23/8/01	Pre harvest				
	30/8/01	Post harvest	*	0 34	NS	0 8
	6/9/01	Post harvest	**	0 22	**	0 18
	19/9/01	Post harvest	*	0 34	**	0 34
	19/9/01	Pre plough				
	5/10/01	Post plough	NS	1 14	NS	0 52
	19/10/01	Post plough	NS	0 59	**	0 1
Wheat	28/8/02	Pre harvest				
	10/9/02	Post harvest	**	0 15	**	0 11
	19/9/02	Post harvest	**	0 07	**	0 09
	18/10/02	Post harvest	*	0 41	**	0 13

* = p < 0 05, ** = p < 0 01, *** = p < 0 001, NS = not significant

6.3.6.2 Species

The partial harvest allowed for continued sampling in the unharvested area between the start of harvesting in July and its completion in August. Over this period a decline in density (P = 0.0073, W = 56) was observed in the dominant species *O. fuscus* whereas the density of *T. tenuis* increased (P = 0.0269, W = 25) and a close to significant increase was observed for *B. gracilis* (0.0513, W = 26.5). Following harvesting in August, the density of *T. tenuis* reduced significantly (P = 0.0041, W = 57) and a close to significant reduction was observed for *B. gracilis* (P = 0.0613, W = 51) with other species showing no significant change.

Prior to the ploughing operation, separate samples were taken from the areas of the field harvested in July and August. The area harvested in July was characterised by a relatively large density of *M. rurestris*. Following ploughing, densities of all species showed no significant change although a close to significant decline (P =0.0533, W = 51) was observed for *M. rurestris*.

Following the harvest in 2002, a significant reduction in density was observed for *T. tenuis* (P = 0.0235, W = 53.5) and *O. fuscus* (P = 0.0163, W = 53.5) with *B. gracilis* showing a close to significant reduction (P = 0.0512, W = 51).

6.4 Discussion

6.4.1 Topping in set-aside

Following the 2001 topping operation adult linyphiids were severely affected with densities being reduced to near zero within two weeks of the operation. Recovery of adults was minimal over subsequent sampling dates. The height of topping of approximately 10 cm could be expected to affect species associated with taller vegetation such as *T tenuis* (Sunderland, Topping *et al* 1996) Whilst this was observed, the epigeic species *O. retusus* was also seen to decline significantly. Nyffeler and Breene (1990) found that mowing of hay meadows negatively affected densities of both foliage and ground dwelling species, including the erigonid species Nyffler and Breene (1990) surmised that between 40% to 50% of the losses observed were not as a direct result of mowing but through subsequent emigration. As removal of the 'upper-storey' vegetation is likely to markedly affect vegetation structure and associated microclimates, the sudden deterioration of habitat quality could have induced both foliage and ground dwelling species to disperse The large but short-lived increase in immature density following topping in 2001 was probably attributed to the hatching and subsequent dispersal of second generation linyphiids

6.4.2 Maize harvest

In contrast to the topping operation, the maize harvest appeared to have a lesser impact on spider densities particularly in the short-term. Relative to pre-operation densities, there was no significant decline and only immatures showed a significant reduction 16 days after harvesting. Declines in the density of immatures were also evident in other fields during this period, possibly though the natural processes of dispersal, recruitment,

and mortality. The rate of decline in immatures was, if anything, rather delayed in maize and wheat.

The relatively elevated cutting height of 15 cm, above which most linyphiids would not be present, could have contributed to the apparent low impact of harvesting. The crop structure of sparse, thick stems may have also been of little value certainly for web-building species. Weeds were probably utilised to a greater extent although their sporadic distribution could have increased sampling error. To some extent densities may also have been buffered by spiders dispersing from earlier harvested crops. Wheat however was harvested approximately a month earlier and much of the subsequent dispersal would likely to have occurred within the period of two weeks following harvesting (see next section).

6.4.3 Wheat / Barley harvest

The reduction in density of adults in the 3 days following cereal harvest was between 41% and 75%. Further declines occurred after this period with adult density being reduced by between 78% and 96 % up to 9 days following harvest. Although Thomas and Jepson (1997) recorded no consistent effects on total spider density before and after cereal harvest, the continuing decline of adults after harvesting observed in this study suggests that emigration was partially responsible for the losses with harvesting eliciting this dispersal. As direct mortality was not measured, the relative importance of emigration to these losses could not be determined. However, a reduction of over 50% between the post-harvest sample taken the day following the partial harvest of Glazeparks, and that taken after 17 days, indicates that, in this instance, emigration was probably of greater importance than direct mortality. Immature densities showed similar

reductions in the short-term, although densities did recover in the earlier harvests of wheat and barley, this being attributable to emergence and dispersal of the second generation at this time.

As the period between harvesting and the first post-harvest sample varied, whether losses of individual species occurred through mortality or emigration could not be determined. For most species non-significant reductions in density were observed during this period. In contrast to other species *T tenuis* showed significant reductions in 3 out of the 5 harvests with *B gracilis* and *O. fuscus* also decreasing significantly in Pitstones. The apparent greater impact on the epiphytic species, *T. tenuis* and *B gracilis*, suggests that these species had an increased likelihood of mortality through the operation and/or were induced to disperse through disturbance and the sudden change in the habitat quality. The presence of these species in a more elevated position within the vegetation (Alderweireldt 1994; Sunderland and Topping 1995) would suggest both circumstances may be plausible. However, sampling efficiency was probably greater for these species given their web site preferences and aggregation in relation to weeds could also have hindered representative sampling in less abundant species making losses harder to quantify.

Evidence of substantial recovery in adults was only observed in the area prematurely harvested in Glazeparks and was probably enhanced by the longer period over which spiders were able to recolonise the area prior to ploughing. Between 26th July and 19th September, adult density recovered to 79% of the pre-harvest density, however the composition of species did vary considerably between the dates with dominance shifting from *O fuscus* in the pre-harvest sample, to *M rurestris* in the sample prior to ploughing. As the majority of *M. rurestris* recorded were from cereals, their increase

may be related to harvest induced dispersal from cereal fields nearby. Senescence of the crop and subsequent loss in habitat quality may also lead to dispersal, (Thomas and Jepson 1999; Weyman and Jepson 1994) and *M. rurestris* could also have migrated from the unharvested area into the harvested area although densities of this species prior to harvesting were not especially high.

6.4.4 Grass harvest

In early May, the first grass harvest in Bigfield and Horse Parks appears to have had little negative impact on spider densities. Densities of the second generation adults were low and declining as is typical during late spring (De Keer and Maelfait 1987b; De Keer and Maelfait 1988b; Dinter 1996; Samu and Szinetar 2002) and immatures rapidly increased, the hatching of the first generation effectively masking any effect of mowing on their densities. The newly established ley in Horse Parks did not support the higher densities seen in Bigfield and, although adults declined significantly, the reduction in adults during the mowing operation was from a very low initial density. The likelihood of significance at this low density was perhaps enhanced by the uniformity in structure of the newly sown ley, and the subsequent lack of aggregation of spiders. No late grass harvest was taken in Horse Parks, the field being turned over to grazing in June.

In contrast to the May harvest, larger reductions in density were observed following the grass harvest in late June. Short term impacts were pronounced with reductions in density of between 77% and 85% of adults occurring within the first 2 days following harvest in 2001. Densities were seen to recover to 61% of the pre-harvest density after 6 days although in 2002 a reduction of 83% was recorded 8 days after harvesting. Many factors are liable to influence the impact of grass-cutting on spider densities, and as

mortality may be influenced by cutting-height and date of harvesting (Nyffeler and Breene 1990), abiotic factors such as light, temperature, humidity, precipitation and wind may all influence the rate at which spiders disperse from the field following harvesting It is expected that these factors will vary year on year as will their effect on rates of dispersal

In 2001 cows were grazing the field from the 8th July and probably contributed to the continuing decline to 96% of pre-harvest density recorded on August 9th. Thomas and Jepson (1997) also found that silage cutting followed by intensive grazing led to near extinction of spider populations in a grass ley.

Lower densities of all species were recorded in the post harvest sample, however in both years the only species which reduced significantly was *B gracilis* As this species tends to be make webs within the vegetation, the harvest may have either reduced numbers directly through mortality or indirectly by disturbance, a change in vegetation structure or other environmental factors which initiated spiders to disperse quickly from the field Thorbek and Bilde (2004) also found that grass cutting was particularly detrimental to *B. gracilis* with relatively high numbers emigrating after the operation. Although little recovery was apparent in adults, early August in both years saw large increases in immatures consistent with the hatching of the second generation immatures.

6.4.5 Ploughing

Grazing in Pitstones, the early period of the year in Eastdown, and, in most cases, harvesting in cereals, all contributed to the relatively low densities of spiders prior to ploughing. Negative impacts were not immediately apparent in any fields and in

Pitstones a significant increase in adult density was observed after 10 days. At such low initial densities the influence of differences in sampling efficiency between grass and bare earth is probably more pronounced and makes this apparent increase questionable. The lack of significant impact however in cereal fields, after approximately the same period, does indicate that ploughing, despite its considerable disturbance through inversion of the surface soil, may not be responsible for immediate and catastrophic declines. Possibly of greater influence on density is subsequent emigration following ploughing and the cumulative effect of further tillage operations. In this study the individual effect of these factors could not be quantified separately. Significant declines were observed with increasing time after ploughing, and also with harrowing and flat-rolling. In maize, although no significant reduction was observed 2 days after ploughing, adults were seen to be significantly lower after 7 days following flat-rolling. Harrowing following ploughing in cereal fields was also associated with a significant reduction in densities though declines may have occurred either through mortality or emigration.

6.4.6 Conclusions

The degree to which spider densities are impacted by farming operations is dependent upon the timing of operations, the length of time between subsequent operations and the type of operation.

The low field density in April and May precluded any large reductions following ploughing and grass harvesting. In contrast the effect of harvesting grass in June and wheat in late August, when densities were relatively high, was more pronounced.

The cumulative effect of a number of operations and practices, such as harvesting followed by tillage, and grass harvesting followed by grazing is seen to dramatically reduce spider densities In Autumn when fields are subject to successive operations leading to a complete loss of vegetation cover and disruption of the soil surface, spider densities are unlikely to recover until the following season. Spiders leaving senescing crops for over-wintering habitats at this time (Rand, Tylianakis *et al* 2006, Thorbek and Bilde 2004) contribute to this lack of recovery.

Where cumulative operations do not occur and some vegetation cover remains, recovery is observed In wheat stubble after an initial decline, both adult and immature density increased to pre-harvesting levels 2 months after harvesting. Maize harvesting may only minimally impact densities owing to the higher cutting height which preserves vegetation cover especially that provided by weeds. Both direct mortality through the action of the harvester and the disturbance induced dispersal are likely to be less severe in this crop under current farming practices.

This study also supports findings from Thorbek and Bilde (2004) where direct mortality from farming operations contributed only partially to overall losses. Emigration through habitat disturbance, enhanced predation and reduced reproduction are suggested as possible causes for continued declines in density following mechanical operations

Chapter 7. General discussion

D-vac sampling in grass proved to be inefficient, with larger spiders being very poorly represented. The problems associated with low suction power have now largely been overcome by use of the modern and more powerful G-vac machines.

The climbing-stick method develops on work by Duffey (1956) who used sticks with adhesive applied to the upper section to trap climbing spiders prior to ballooning. In developing this method, the addition of the net and bottle-trap have the benefit of both increasing catch size and reducing the processing time in sorting captured spiders. This method has advantages over alternatives such as deposition traps which can be dried out in hot weather, or diluted in wet weather, reducing their efficacy. Deposition traps may also produce considerable amounts of by-catch which can make sorting arduous. Although ballooning activity is observed to reflect changes in ground populations (Thomas and Jepson 1999; Weyman, Jepson *et al.* 1995), these traps may not demonstrate this relationship when ground populations are sampled alongside traps at the field scale. A possible reason for this is that a substantial proportion of the catch is thought to originate from intercepted spiders from the wider area and abundance of species sampled locally may not reflect abundance at the landscape scale.

Because of the potentially large catch sizes, traps need to be emptied daily to prevent silk build-up. Where sites are to be visited infrequently, deposition traps may be more appropriate or alternatively the interception of spiders could be reduced by removing nets from climbing-sticks.

From a recent examination of ballooning survey data, obtained over eleven years from a 12.2 m Rothamsted suction trap (Macaulay, Tatchell *et al* 1988) in Switzerland, Blandenier (2009) noted the maximal numbers of individuals ballooning were recorded in late spring and summer, between the end of May and mid August Reduced activity was observed between the beginning of December and the end of February These findings contrast with the phenology recorded from the 'stick and bottle' traps used in this study where maximal numbers occurred between November and February with comparatively little dispersal over the spring and summer. A discrepancy between trapping methods was also noted by Toft (1995a) in Denmark Spiders sampled using a 12.2 m suction trap were observed to peak in late summer with low catches in early spring and autumn. In contrast, spiders collected from a 1 m high wire fence had two maxima, one in early spring and one in autumn Toft suggested that during these periods the majority of dispersal occurred through short duration flights close to the surface or through movement across the ground via bridging threads. Higher and longer dispersal was thought to predominate instead in the late summer period. The explanation given by Toft is that on clear nights in autumn, net loss of radiation from the ground (negative radiation balance) leads to the creation of a stable cold surface layer of air (inversion layer). Following sunrise, heating of the surface begins to erode the nocturnal surface inversion forming a shallow, mixed layer with the remaining inversion above Spiders ballooning in these conditions rise only as far as the stable layer before being carried horizontally, alighting on the ground again after a short distance In summer when the radiation balance is positive, the conditions for forming surface inversions are mostly absent and radiative heating leads to buoyancy of the air mass which, unimpeded, allows ballooning spiders to reach greater heights.

Thorbek *et al.* (2002) found a strong correlation between numbers of ballooning spiders sampled at the same location by 1.4 m and 12.2 m suction traps, with the 1.4 m trap catching consistently higher numbers. From the proportions of spiders caught in each trap over the sampling period, it was surmised that the seasonal pattern of changes in dispersal height observed by Toft (1995a) did not apply to the UK. However, from the data presented on the relationship between suction trap catches (given as 12.2 m/(12.2 m +1.4 m)), the majority of the total weekly catches where spiders were recorded only in the 1.4 m trap appear to occur between December and March (one other in May). The only incidences of spiders only being sampled by the 12.2 m trap also occur between December and February, however these are fewer than the opposite situation. As no quantitative data on numbers caught is given for the winter period, the actual numbers trapped at high or low-level cannot be evaluated. However, these winter anomalies could suggest a reduced mixing of the near-ground air mass during some periods of the winter months.

Toft (1995a) suggested that ballooning close to the ground, or at height, might serve different purposes. Short-distance dispersal could be an adaptive behaviour related to the need to seek overwintering sites away from ancestral habitats that were periodically flooded. If this is a common phenomenon of dispersal in farmland agrobionts, then attributing a seasonal purpose to such dispersal may be unnecessary, and this behaviour is perhaps in agreement with ESS strategy proposed by Weyman *et al.* (2002). The presence of spiders ballooning at low-level could be a consequence of the limited period over which ballooning activity occurs on days when conditions are suitable. As the inversion layer breaks down, spiders might be expected to gain height after initially being concentrated nearer the ground. If ballooning activity tends to occur before 13:00 (Thorbek, Topping *et al.* 2002) then numbers ballooning when the inversion layer

finally erodes could be lower overall, and therefore proportionally less are then sampled at height when the air mass becomes more mixed These numbers could be further constrained by the later sunrise in autumn. For agrobiont linyphiids low-level dispersal could serve the same functionality as ballooning in summer, this being an adaptive response to environmental unpredictability Agrobiont linyphiid spiders may then be, for the most part, behaviourally 'aseasonal' in their dispersal response, though the nature of their dispersal could be determined by the prevailing meteorological conditions of the season or those prevalent at a particular location

Sampling at a greater height will always sample fewer dispersing spiders if the majority of ballooning occurs closer to ground However, traps, where the greater part of the catch comprises intercepted spiders, could also underestimate dispersal when vertical rather than lateral movement of ballooning spiders is enhanced. Further observations on seasonal ballooning data may confirm if seasonal discrepancies in ballooning activity are a common feature of using different sampling methods, particularly when samples are taken at different heights Aspects of the local sampling conditions - whether the study site is in a sheltered valley area, in a rural locale or near to a large conurbation, should be taken into account as sampling location could have implications for the degree of mixing of the near-ground, air mass with respect to seasonal conditions.

Toft (1995a) also suggested low-level ballooning in the autumn was responsible for mass dispersal events, where dense gossamer is seen to cover the ground, as this could reflect multiple ballooning attempts or bridging when higher-level dispersal was restricted. Although this could be a contributing factor, high population density and the concentration of spiders into undisturbed fields after harvesting could also be

significant. A common initiating factor must also be present to entrain the ballooning response and make spiders more likely to balloon en masse (Bell, Bohan *et al.* 2005).

Previous european-based studies which have sought to measure ballooning activity in the field (usually to investigate specific hypotheses) have looked at the total number of spiders undifferentiated by species (Sunderland and Topping 1993; Toft 1995a; Weyman, Jepson *et al.* 1995), or have concentrated on few or single species (De Keer and Maelfait 1987b; De Keer and Maelfait 1988b; Topping and Sunderland 1998; Wingerden van 1977; Wingerden van 1980), or have had a restricted sampling period over which the spiders were collected (Thomas and Jepson 1999). As previous mentioned, the most detailed study to date on species-specific ballooning activity over time refers to samples collected by the Rothamsted suction trap (Blandenier 2009; Blandenier and Fürst 1997) which could possibly show a different seasonal bias to the trapping method used here.

Using the 'stick and bottle' traps, samples collected in this study have provided data on the ballooning activity of spiders dispersing over agricultural land for a period of 18 months. The different sampling methods used in other studies make comparisons difficult although peak dispersal times are in broad agreement with Duffey (1956) and support the general consensus that dispersal activity of common linyphiids tends to occur in the autumn, winter and spring periods. As expected, the largest peaks in dispersal activity coincide with periods of relatively low wind speed. Previous observations that *Erigone* species balloon more frequently than other linyphiids (Weyman, Sunderland *et al.* 2002) are also confirmed by this study. Dispersal activity was observed to be more similar for closely related species in the genera *Erigone* and *Oedothorax*, and also for more distantly related members of the linyphiinae, *L. tenuis*

and *B gracilis* This appears to demonstrate that the deterministic processes of when to balloon show a strong genetic predisposition at the species and genus level with probability distributions governing the proportions of individuals ballooning having greater similarity in closely related species.

The determination of seasonal differences in ballooning motivation observed for *E atra* was probably confounded by variable temperatures exposed to the test subjects. Dispersal activity was however observed to occur in all months suggesting that a strong seasonal variation in ballooning motivation was absent and to this extent results were not in conflict with the findings of Weyman *et al* (1995) The failure to elicit a pre-ballooning response in the wind chamber for the *Oedothorax* spp. suggests that either a different mechanism or different threshold values exist which initiate ballooning in this species compared to *Erigone* spp. *Oedothorax* spp. were also observed to balloon less frequently than *Erigone* spp. in the field although very pronounced dispersal was also observed for some days Further examination of the preceding and prevailing meteorological conditions could give an explanation as to the possible stimuli initiating ballooning in *Oedothorax* Photoperiod has been suggested as influential for reproduction in some studies (albeit tentatively) (Schaefer 1977, Thorbek and Bilde 2004), however, De Keer and Maelfait (1987a) found little evidence for photoperiod influencing reproduction or development in *O fuscus* in the laboratory. The 'male-only' dispersal peak in October may also indicate differences in motivation for ballooning in sexually mature adults. Studies on linyphiids in the literature have tended to concentrate on *Erigone* species or *L tenuis* Further study of *Oedothorax* spp. could be beneficial in providing a comparative model of behavioural traits present in pioneer spider species.

The ballooning pattern observed for the tetragnathid spider, *P. degeeri*, is notable in that it occurs in a narrow period between October and November in both years and appears to fall outside the period of highest population density. That dispersal activity is to a large extent only observed in adults is unusual in that many other spiders tend to either disperse as immatures, or during both their immature and adult phases, as in the linyphiids (Bell, Bohan *et al.* 2005). From the development times given by Alderweireldt and De Keer (1990), much of the later brood whose eggsacs were laid in July, may be expected to have already reached maturity and therefore the final moult is probably not a stimulus for dispersal. The behavioural shift from the rather sedentary web-spinning immatures to cursorial adults (Alderweireldt and De Keer 1990; Roberts 1995) could be significant although the specificity of the dispersal period perhaps points to a precise deterministic cue such as photoperiod.

From the initial monitoring of spider populations, the study site is typical of most other agricultural landscapes studied in northern Europe, with several typical agrobiont species being present in abundance. *Oedothorax fuscus* is the dominant linyphiid species in most disturbed habitats irrespective of field use. This could be due to a particular affinity for grazed pasture land of which there is a high proportion in the southwest UK landscape. De Keer and Maelfait (1987b) noted that *O. fuscus* 'thrived' in intensively grazed pasture. Although this is an unqualified statement it would be interesting to see if *O. fuscus* is found in the same dominance in pasture in a more arable setting. Other spiders known to be numerous in cereal dominated regions such as *M. rurestris* (C. F. G. Thomas pers. comm.) were found in comparatively modest numbers at the study site. Another *Oedothorax* species, *O. apicatus*, is also found abundantly in arable situations in the UK, however no single *O. apicatus* specimen was found during the study which could be due to this species having a more easterly distribution. As

observed in this study, *E atra* and *E dentipalpis* are commonly found in the same agricultural habitats although some degree of habitat preference could be apparent (Downie, Ribera *et al* 2000). It would be of interest to discover why in passively dispersing species with abundant populations on agricultural land, *Oedothorax* species are regionally separated. Climate could be a mediating factor as could competitive exclusion From the example of *E atra* and *E. dentipalpis* this would appear unlikely, however in less frequently dispersive species, such as those of the genus *Oedothorax*, competition may perhaps be more influential in determining geographical location.

The presence of higher abundances of *L tenuis* in wheat is in general agreement with the literature (Sunderland 1996). To some extent epigeic species may have been underestimated in grass leys owing to the inefficiency of the D-vac sampler The degree to which differences in assemblages between crops are brought about by immigration is unknown although no large dispersal events were observed during the summer period. As has been observed for *L tenuis* (Topping and Sunderland 1998) favourable environments for certain species are likely to be reflected in their reproductive success and overall differences in abundance are probably a result of population growth over the summer period.

Apart from early grass cutting, farming operations in grass and cereal fields, had negative impacts on spider populations. The results generally corroborate the findings of Thorbek and Bilde (2004), that population declines also occur after farming operations, and therefore are not exclusively caused by mortality due to direct mechanical disturbance Emigration and factors increasing mortality in the remaining population are potentially responsible In contrast to other operations, harvesting in maize was relatively benign and densities remained relatively high over the winter months

7.1 Further work

Only a limited number of species are dominant on agricultural land, and therefore it should be an achievable aim to provide accurate species specific information that can be used in future simulation studies. Such studies could indicate if future landscape change could be detrimental to particular species. The abundance of common agrobionts is dependant on the 'balance' in the landscape of primary farmland habitat and non-crop habitats such that a shift too far in the proportion of either habitat may lead to a reduction in the overall agrobiont population. Landscape based studies have supported this (Schmidt, Thies *et al.* 2008), but development of computer simulation of landscapes may prove valuable for long-term predictions especially given the potential for rapid climate change, and the implications for farming.

Further knowledge of the influence of environment, physiology and genetics are required to address why ballooning propensity may differ between individuals, over time, and indeed between sexes. For insects comparatively far more work has been conducted into the physiological processes associated with dispersal. For instance changes in the level of Juvenile Hormone (Herman and Tatar 2001) and the neurotransmitter Serotonin (Guerra, Steger *et al.* 1991; M.L. Anstey, S.M. Rogers *et al.* 2009) have been seen to correspond with the timing of dispersal and dispersal related processes in some species. Insect life-histories often display distinct changes in morphology, feeding and dispersal behaviour, and therefore changes in physiological state between developing instars and the imago are likely to be similarly distinct. Spiders in contrast tend to be morphologically and behaviourally similar as juvenile and adults. Sexual maturation however does result in specific behaviours being expressed. Edysteriods present in insects, arachnids and crustaceans as the principal moulting

hormone have been shown to influence sexual behaviour in female *Tegenaria atrica* (Trabalon, Niogret *et al.* 2005). These hormones have also been suggested as a possible candidate for sex hormones in insects (De Loof 2006). Levels of neurotransmitters in male *Anphonophelma hentzi* (Girard 1854) differ between dominant and subordinate (Punzo and Punzo 2001) spiders suggesting that previous agonistic encounters could influence future behaviour It could also be possible that neurochemical differences exist in spiders with different mating histories which in turn could have behavioural implications At present the majority of research into ballooning variation is observational and similar work should to be performed on spiders, as has been achieved for insects, to discover the neurological and endocrinological basis to dispersal This will assist in determining how ballooning propensity may alter between individuals, and gender, and the potential heritability of such variation (Bonte, De Clercq *et al* 2009).

Chapter 8. References

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Chapter 9. Appendices

Appendix 1

Appendix 9-1. Species list of spiders collected from climbing stick traps (Chapter 6) and number of adults sampled. Numbers may not reflect total for family. Lycosidae and Thomisidae disperse mainly as immatures.

Linyphiidae	Nº sampled
Oedothorax fuscus (Blackwall)	6732
Erigone atra (Blackwall)	4502
Milleriana inerrans (O.P.-Cambridge)	3751
Tenuiphantes tenuis (Blackwall)	1825
Bathyphantes gracilis (Blackwall)	1532
Erigone dentipalpis (Wider)	897
Oedothorax retusus (Westring)	449
Savignia frontata (Blackwall)	152
Pelecopsis parallela (Wider)	78
Meioneta rurestris (C.L. Koch)	47
Walckenaeria vigilax Blackwall	44
Porhomma microphthalmum (O.P.-Cambridge)	43
Centromerita concinna (Thorell)	39
Centromerita bicolor (Blackwall)	17
Hypomma bituberculatum (Wider)	12
Mioxena blanda Simon	9
Diplostyla concolor Emerton	8
Gongylidiellum vivum (O.P.-Cambridge)	7
Tenuiphantes flavipes (Blackwall)	6
Micrargus subequalis (Westring)	6
Walckenaeria antica Wider	5
Tenuiphantes zimmermanni Bertkau	4
Neriene clathrata (Sundevall)	4
Tenuiphantes ericaeus (Blackwall)	4
Ostearius melanopygius (O.P.-Cambridge)	3
Porhomma pygmaeum (Blackwall)	2
Ceratinopsis stativa (Simon)	2
Monocephalus castaneipes (Simon)	2
Erigone promiscua (O.P.- Cambridge)	1
Microctenonyx subitaneus (O.P.-Cambridge)	1
Cnephalocotes obscurus (Blackwall)	1
Monocephalus fuscipes (Blackwall)	1
Taranucnus setosa (O.P.-Cambridge)	1
Dicymbium nigrum (Blackwall)	1
Microlinyphia pusilla (Sundevall)	1
Centromerus dilutus (O.P.-Cambridge)	1
Tenuiphantes minutus (Blackwall)	1
Tenuiphantes mengei Kulczynski	1

Theridiidae	Nº sampled	
Robertus arundineti (O.P-Cambridge)	450	
Robertus neglectus (O.P-Cambridge)	21	
Theridion pallens Blackwall	8	
Achaearanea simulans (Thorell)	2	
Enoplognatha ovata (Clerck)	2	
Anelosimus vittatus (C. L. Koch)	2	
Anelosimus aulicus (C. L. Koch)	1	
Theridion mystaceum L. Koch	1	
Theridion sisyphium (Clerck)	1	
Theridion varians Hahn	1	
Episinus angulatus (Blackwall)	1	Imm.
Tetragnathidae		
Pachygnatha degeeri Sundevall	351	
Pachygnatha clercki Sundevall	10	
Tetragnatha obtusa (C.L. Koch)	1	
Mimetidae		
Ero cambridgei Kulczynski	5	
Thomisidae		
Xysticus cristatus (Clerck)	4	
Philodromus albidus Kulczynski	3	
Philodromus collinus C. L. Koch	1	
Araneidae		
Larinioides cornutus (Clerck)	4	
Nuctenea umbractica (Clerck)	1	Imm.
Clubionidae		
Clubiona diversa O.P.-Cambridge	3	
Pisauridae		
Pisaura mirabilis (Clerck)	2	
Dictynidae		
Dictyna uncinata Thorell	1	
Nigma puella (Simon)	1	
Lycosidae	no adults identified	

Appendix 2

Appendix 9-2 Published - Woolley C, Thomas CFG, Hutchings L, Goodacre S, Hewitt GM, Brooks SP (2007) A novel trap to capture ballooning spiders *The Journal of Arachnology* **35**, 307-312

2007. The Journal of Arachnology 35:307–312

A NOVEL TRAP TO CAPTURE BALLOONING SPIDERS

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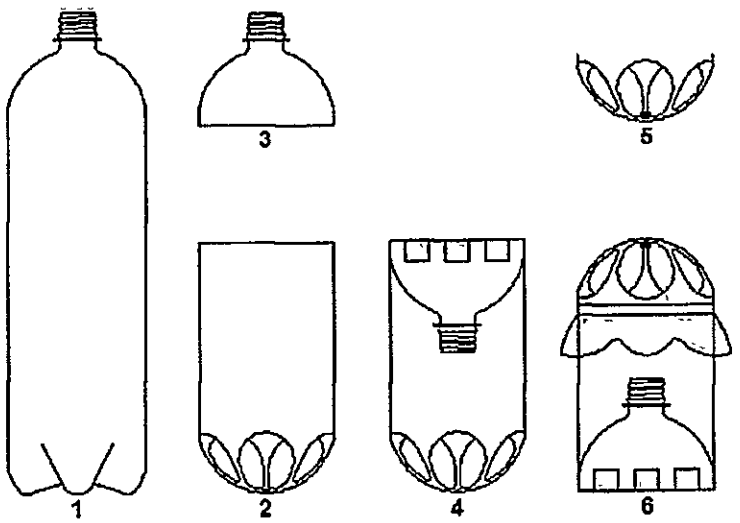
ABSTRACT. An unattended trap was designed to sample and retain spiders dispersing from agricultural grassland and crops. Traps comprised a removable bottle-trap fixed to the top of a vertical metal rod or "climbing-stick" that spiders climbed during normal pre-ballooning behavior. Bottle-traps caught over eight times more spiders than sticks treated with insect trapping adhesive. Draping sticks with nets increased the effective area of the traps and increased the catch size threefold. On average, 9.1% of spiders were lost from traps during the daytime sampling period. No difference in average rate of loss of spiders from the bottle-traps was observed between night and daylight hours. The bottle-trap design is economical and simple to construct, erect and operate. Continuous sampling also allows multiple traps to be used simultaneously in various locations.

Keywords: Aerial dispersal, sampling, bottle-trap, climbing-stick

Aerial dispersal by ballooning is a key strategy in the life histories of many spiders, especially pioneers of disturbed, patchy habitats exemplified by linyphiids in agricultural landscapes (Thomas et al. 2003a). Quantifying the dispersal power of these species is a necessary prerequisite for accurately modeling spatial population dynamics and developing successful sustainable management strategies. Various techniques that actively or passively intercept airborne spiders have been used to measure aspects of aerial dispersal. For example: the use of nets and sticky traps to measure aerial density at one or more altitudes (Greenstone et al. 1987; Greenstone 1991; Thomas et al. 2003b); manual collection from fences, wire, or string to quantify numbers passing a point or line per unit time (Vugts & Van Wingerden 1976; Thomas et al. 2003b); or water traps to quantify deposition rates per unit area (Weyman et al. 1995; Thomas & Jepson 1999). These methods are either labor intensive, require operator attendance, cannot easily sample several locations at the same time, or may be cumbersome or expensive.

An alternative sampling method exploits the climbing behavior normally exhibited by spiders as a precursor to ballooning (Blackwall 1827): spiders climb to a high point where a silk line can be produced above the surrounding vegetation and where suitable atmospheric conditions for successful ballooning are likely to occur (Suter 1999). Sticks, canes or similar objects inserted into the ground, provide artificial platforms that stand higher than the surrounding vegetation. Spiders climbing and attempting to balloon from these can be observed, or caught and counted, to give a relative indication of ballooning activity over a given period. Thorbek et al. (2002), in a validation of this technique, found that numbers of spiders observed climbing a 30 cm stick correlated well with numbers obtained from an aerial suction trap. Using a similar technique to sample several habitats over time, Duffey (1956) applied a tacky adhesive to the tops of canes to trap climbing spiders. However, the adhesive was adversely affected by hot, cold or wet weather and became clogged with winged insects during summer months.

This paper describes and evaluates a novel



Figures 1–6—Trap construction. 1. Two liter soft-drinks bottle. 2. Bottle bottom with the five reinforcements removed. 3 Top removed and section below discarded. 4. Inverted top inserted into the remaining section and secured with adhesive tape. 5. Screw cap glued underneath the central hub. 6. Finished trap with fine gauze fastened in place with a rubber band.

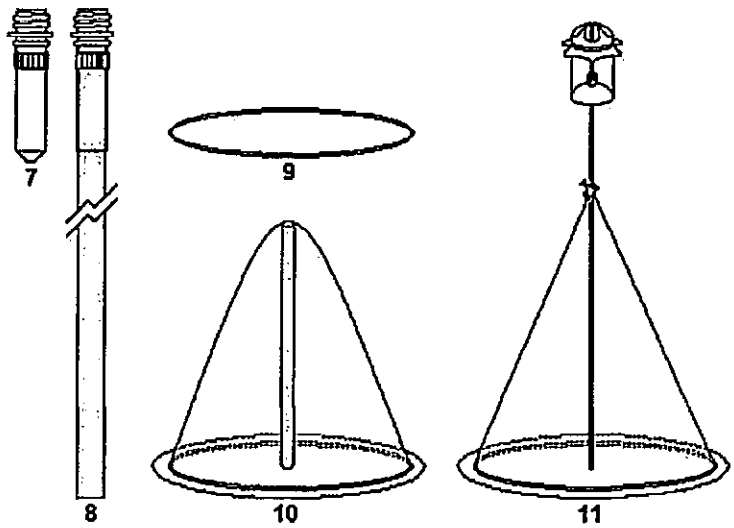
design that develops the climbing-stick into a trap to allow continuous unattended sampling without the use of adhesive. Attached to the top of a climbing-stick is a "bottle-trap" operating on the lobster-pot principle. Climbing spiders are retained within the bottle-trap until it is removed or replaced. In the present paper we compare the trapping efficiencies of climbing sticks either with bottle-traps or with adhesive.

The trap collects spiders climbing from the underlying vegetation before they first become airborne, and spiders already airborne arriving at the trap from sources upwind. In the present paper we do not differentiate between these two potential sources However, we evaluate the effect of suspending a net skirt from the climbing-stick to increase the effective vertical and horizontal cross-sectional area of the trap. This increases both the source area of spiders emerging from the ground and the interception of airborne spiders.

METHODS

Trap construction.—The "lobster-pot" part comprising the bottle-trap was constructed from a standard straight-sided, clear plastic, 2-liter soft-drinks bottle (Fig. 1). The body of the trap was made by first removing, with a heated scalpel blade, the material between the five reinforcing moldings in the base (Fig 2). The top section of the bottle was then removed, just below the shoulder, approximately 9 cm from the top of the bottle opening (Fig. 3). A band approximately 7 cm deep was cut away from the main body and discarded. The removed top section was then inverted and fixed into the remaining base section of the bottle using adhesive tape (Fig. 4), ensuring no gaps remained between the two sections A 2 ml micro-tube screw-cap (Sarstedt®, A.G. Sarstedt & Co. Nümbrecht, Germany) was glued with super-glue (Loctite®, Henkel, Düsseldorf, Germany) centrally beneath the now inverted base section and above the original bottle top opening forming the new base (Fig. 5). A 20 × 20 cm square of white voile gauze fabric was then fastened tightly over the five cut-away openings with a rubber band (Fig. 6). The cut-away openings covered in fine gauze voile material allowed vertical air flow, general ventilation and, when removed, the extraction of spiders from the trap

The climbing-stick was made from a 1.5 m length of 7.9 mm diameter aluminum rod. The surface was roughened with sandpaper to assist climbing spiders.



Figures 7–11.—Trap construction. 7. Micro-tube. 8. Micro-tube with bottom removed, pushed over the end of the climbing-stick and glued in position. 9. Circular wire frame. 10. Netting pulled over pole with circular wire frame placed over netting. 11. Finished trap with bottle-trap screwed on and net clipped to stick.

An attachment for the bottle-trap was made using the body of the 2 ml micro-tube from which came the cap that had been glued to the bottle-trap. The bottom section of the main body was removed just above the taper (Fig. 7). A small amount of rapid drying epoxy resin (Araldite®, Huntsman Advanced Materials, Everberg, Belgium) was applied to the inside of the tube, which was then placed over the end of the climbing-stick with the thread end uppermost and extending approximately 5 mm above the end (Fig. 8).

The net was constructed from 2 cm mesh bird netting made from a natural-fibre twine. Sufficient material to form a small tent was draped over a 1.2 m wooden pole. A 3.14 m length of 2 mm fencing wire, formed into a 1 m diameter circle (Fig. 9) was placed over the netting and pole to weigh down the base of the net and keep it splayed out. The netting was pulled taut over the pole, arranged evenly around the frame, and its hem secured to the circular base with wire ties before cutting away excess material. (Fig. 10).

Setting and operating the trap.—To set the trap, the climbing-stick was pushed vertically into the ground, and a bottle-trap placed over and screwed to the top of the stick. If a net was also used, this was first pulled up to form a cone and the climbing-stick placed through the apex before the stick was pushed into the ground. The net was then clipped to the stick using a small bulldog clip set at an angle to ensure the spiders continued climbing. The circular wire base was held down with wire pegs or stones. The bottle-trap was then screwed to the top of the stick (Fig. 11).

For continual sampling, bottle-traps were unscrewed and replaced with empty ones. For daily samples reported here, traps were typically changed each evening after ballooning behavior had finished. Removed traps were placed in plastic bags in the field before returning to the lab. Spiders were extracted from traps by removing the voile gauze and shaking vigorously over a tray from which spiders were collected with an aspirator. Any spiders remaining in the trap were removed either with an aspirator or, if there was a lot of silk in the trap, with a small paint brush.

Trap evaluation.—Experiments were performed with traps set along a transect in an 8 ha grass field on the estate farm at the Seale-Hayne Faculty, Newton Abbot, Devon, in the southwest of the UK. The temporary grass ley was approximately 150 mm tall at the time of sampling. The transect, orientated north-south, traversed the brow of a hill, the mid-section

Table 1.—Total number of spiders caught per trap over an 11 day period from climbing-sticks with bottle-traps and climbing-sticks with adhesive.

Trap number	1	2	3	4	5	6	7	8	9	10
Bottle-trap	18	17	14	46	78	107	131	75	53	25
Adhesive	1	6	8	9	6	5	16	7	8	0

being elevated relative to the extremities. An electric fence was used to protect the transect from disturbance by sheep and cattle that periodically grazed the field.

Three aspects of the trap were evaluated: catch size from climbing-sticks with bottle-traps compared with climbing-sticks with a polybutene-based insect trapping adhesive (Oecotak A5®, Oecos Ltd, Kimpton, Hertfordshire, England) applied to the uppermost 15 cm of the stick; catch size from climbing-sticks and bottle-traps with and without nets; retention of spiders left in bottle-traps during the day and overnight.

To compare catch size from climbing-sticks with either bottle-traps or adhesive, 10 traps of each design were set alternately at 10 m intervals. Bottle-traps were emptied on each of 11 successive days in March 2003; climbing-sticks with adhesive accumulated spiders over the same period. Climbing sticks with adhesive were checked periodically to ensure that the accumulation of trapped spiders or insects was not excessive and that there was ample exposed adhesive to maintain capture efficiency. Total numbers caught per trap were recorded at the end of the sampling period. For catch size evaluations comparing climbing-sticks and bottle-traps with and without nets, 10 traps of each design were set alternately at 10 m intervals. Samples were taken and recorded daily over a 13 day period in March 2004. For the retention study, 10 climbing-sticks with bottle-traps were placed in the field as above. Numbers of spiders in each bottle-trap were recorded after 24 h at 17:00. Traps were then relocated to a tarmac substrate away from ground vegetation to minimize further ingress of spiders. Numbers of spiders remaining in the traps were again recorded at 09.00 and at 17.00 the following day.

RESULTS

Comparison between climbing-sticks with bottle-traps and climbing-sticks with adhesive.—For all traps, catch sizes were higher for climbing-sticks with bottle-traps than for climbing-sticks with adhesive (Table 1). Total catch size over the period for climbing-sticks with bottle-traps was 564 spiders and for climbing-sticks with adhesive, 66 spiders.

Comparison between bottle-traps with and without nets.—Climbing-sticks with nets caught greater numbers of spiders than those without nets for 7 days out of the 13 day period (Table 2). Spiders were not recorded in any trap on 22, 23, 24, 28, and 29 March when high wind speeds suppressed ballooning activity. No differences were recorded on 26 March though catch size was very low with only 2 spiders recorded in all traps together. The total numbers of spiders caught by climbing-sticks with and without nets were 641 and 218 respectively.

Retention of spiders in bottle-traps.—Of a total of 413 spiders in 10 bottle-traps recorded at 17:00, 69 (15.3% ± 11.8%) had escaped by 09:00 the following morning. A further 35 (9.1% ± 7.7%) escaped between 09.00 and 17:00. The average loss over 24 h was 24.4% ± 16.6%. A significant linear regression (adjusted R^2 = 63.6%, P = 0.004) between initial numbers caught and numbers lost after 24 h indicated losses to be largely den-

Table 2.—Daily totals of spiders caught for all traps with and without nets.

Date	18/3	19/3	20/3	21/3	22/3	23/3	24/3	25/3	26/3	27/3	28/3	29/3	30/3
Nets	14	324	41	46	0	0	0	147	4	1	0	0	64
No nets	2	137	8	7	0	0	0	57	1	1	0	0	5

sity independent. Mean rate of loss (± SE) from traps between 17:00 and 09:00 was 0.431 ± 0.141 spiders per hour and from 09:00 to 17:00, 0.438 ± 0.148 spiders per hour. No significant difference in rate of loss was observed between night and day hours ($F_{(1,18)} = 0.01$, $P = 0.976$).

DISCUSSION

Climbing-sticks with bottle-traps are extremely effective, cheap and easy to make and use. We estimate the cost of construction materials to be less than $9 US per trap at current prices. Apart from the greater catch size, which, in total, was over eight times that of climbing sticks with adhesive, the bottle-traps also retain the advantage of easy replication and the ability to simultaneously sample different habitats at large spatial and/or short temporal scales. The retention of live spiders means trapping agents such as adhesive or water and detergent are not required. Furthermore, additional behavioral, ecological or genetic studies can be carried out on the trapped spiders if required.

The addition of nets to climbing sticks with bottle traps increased catch size almost three fold. The trials reported here were conducted in short grass. However, in other trials conducted in taller crops, such as wheat, it was necessary to use 2.5 m climbing-sticks to raise the nets and bottle-traps above the crop in order to intercept airborne spiders. For comparative work sampling airborne spiders above crops of differing height, traps should be set at a constant height above the roughness length of the vegetation.

Although losses from traps left operating for several consecutive days can be estimated, it is recommended that the traps are emptied daily, unless spiders are being collected only for laboratory studies. This avoids large amounts of silk accumulating inside the bottle-traps which makes separation of the spiders from the silk difficult and extraction much more time-consuming. Similarly, when large numbers of spiders were caught within a single day, we found traps were best emptied immediately after collection because of the quantity of silk produced if left overnight. We found traps were best removed in the evening after ballooning had finished. If traps cannot be changed until the morning, it should be carried out very early during summer months in order to prevent cross contamination with the previous day's sample. If longer duration sampling is required and live spiders are not, a preserving fluid could be introduced into the bottom section of the bottle-trap. Spiders would fall into this, thereby reducing losses and minimizing any build-up of silk.

A large variation in catch size was observed along the transect, particularly for the bottle-traps. This was possibly due to the greater trapping efficiency of the bottle-traps coupled with the undulating nature of the field, the greatest catch size being recorded at the highest elevation.

Linyphiids were by far the commonest spiders caught by the traps, being highest both in numbers and in occurrence throughout the year. Other spiders caught in lesser numbers belonged to the families Thomisidae and Araneidae. Though immature thomisids were observed ballooning, adults of these families may have been present in traps as an accident of other behaviours such as rigging, locating shelter/feeding sites or web building. Care must therefore be taken before attributing dispersal by ballooning to all spiders caught.

The bottle-traps sometimes caught other insects including bush crickets, cantharid beetles, ephemeropterans, plecopterans, tipulids and various other dipterans. Some of this bycatch might prey on spiders but we did not see any evidence for this. Other potential losses are likely from predation among spiders but this was not quantified and is likely only if traps are left operating unchanged for longer periods.

ACKNOWLEDGMENTS

This work was funded through BBSRC grants D14032, D20476 and D14036. We would like to thank all the technical and farm staff at Seale-Hayne for their assistance in this work.

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Manuscript received 5 June 2006, revised 27 January 2007.

Appendix 3

Appendix 9-3. Published - Thomas CFG, Blackshaw RP, Hutchings L, Woolley C, Goodacre S, Hewitt GM, Ibrahim K, Brooks SP, Harrington R (2003) Modelling life-history / dispersal-strategy interactions to predict and manage linyphiid spider diversity in agricultural landscapes. In 'Proceedings of the 1st Landscape management for Functional Biodiversity Study Group'. Bologna (Italy). (Eds W A.H., H-MP Rossing and G Burgio) pp. 167-172. (IOBC wprs Bulletin).

Modelling life-history / dispersal-strategy interactions to predict and manage linyphiid spider diversity in agricultural landscapes

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Abstract: Linyphiid spiders are an ideal model for studying spatially dynamic ecological processes at a landscape scale. They are important predators of small invertebrates such as cereal aphids and other agricultural pests but are also susceptible to agrochemical treatments and other farming practices. Being able to move large distances on the wind by "ballooning" they spread risks by dispersing between the shifting resources and hazards in the farmland mosaic. We hypothesise that their life histories and dispersal strategies interact with patterns of land use to determine the population size and persistence of different species, hence diversity of the group as a whole in agricultural landscapes.

This paper describes an on-going project that will use non-linear modelling to link wind-borne dispersal, population dynamics, habitat dynamics and landscape structure in simulation models. Although no results are available at this stage, we describe some methods and approaches adopted for model parameterisation with population and dispersal data, land use data and meteorological records. Model testing and validation using historical records and population genetic data of spiders sampled from various locations are also described. When fully developed, the models will be used to assess risks to regional biodiversity from local field practices and so aid the development of sustainable agricultural systems.

Key words: aerial dispersal, risk-spreading, fragmented habitats, mtDNA, microsatellite, MCMC

Introduction

The abundance and diversity of many farmland invertebrates are in a state of chronic decline (Aebischer, 1990). In order to assess the risks that modern agriculture poses to the persistence and maintenance of diversity, and to develop agricultural systems that ameliorate them, it is necessary to understand the ways in which land use at the field scale affects these populations at the landscape scale.

Agricultural landscapes are fragmented in space and time to form a shifting mosaic of ephemeral habitat patches. These are characterised by the various resources associated with crops in rotation, and the risks of exposure to catastrophic disturbances from events such as insecticide use, harvesting of crops and cultivations. Many farmland invertebrates are well adapted to agricultural landscapes by being highly dispersive enabling them to exploit patchy resources and escape perturbations within this shifting mosaic. In such a dynamic system, population persistence at the regional or landscape scale is likely to result from dispersal and life-history strategies that conform to the spreading of risk paradigm (den Boer, 1998). Dispersal, however, is inherently risky and, in evolutionary recent history, insecticides form a new hazard to which many farmland species are exposed. It is unlikely that invertebrates have been able to adapt their dispersal and life history strategies to cope with these additional hazards in such a short time, and this is likely to be partly responsible for the observed population declines. However, it is possible that in some environments lower dispersal rates have been selected, for example in island populations where the risk of dispersing into the sea has been a significant, long-term hazard.

Many models have demonstrated the theoretical importance of habitat spatial structure and dispersal to population persistence. However, few models are parameterised or validated with reliable field data to test theory (Dieckmann, *et al.*, 1999). In particular, there are few models of species that inhabit or are affected by agricultural systems, or that test the effects of experimentally manipulated patterns of land use on population persistence and diversity. There are four main areas of information that need to be integrated in order to understand and model the population processes at the landscape scale: landscape structure, patch dynamics within the landscape structure, population dynamics within habitat patches, and dispersal dynamics between the patches. Linyphiids or "money spider" (Araneae, Linyphiidae) are important aphid predators in agroecosystems (Sunderland *et al.*, 1986) and are an

ideal group for studying and modelling population persistence and the maintenance of diversity because detailed information can be acquired on all four components of the system

Most theoretical studies fail to transfer to practical testing and application because of difficulties associated with quantifying species' dispersal (Dieckmann, *et al*, 1999) Critically, many linyphiid species disperse on silk filaments (ballooning) by the same wind-borne mechanism in a well defined "weather window" or wind-speeds below 3 m/s^{-1} Other aspects of dispersal behaviour are easily quantifiable in simple wind-chamber experiments (Weyman *et al*, 1995) or are governed by meteorological conditions that are easily measured or obtained from archived sources Linyphiids are thus able to disperse frequently and redistribute populations over wider areas Other useful characteristics of linyphiids include the ease with which they are sampled in the field and reared in culture to determine the effects of habitat disturbance and life-history parameters (DeKeer & Maelfait, 1998, Thomas & Jepson, 1997) Furthermore, several linyphiid species with different life history and dispersal strategies (e g reproductive rate, age of dispersal, probability of dispersal, number of flights) can be selected for study from the same farmland habitats

In a recent study (Halley *et al*, 1996) estimates of reproductive rates and habitat disturbance effects in a few cereal and grassland habitats (Thomas & Jepson, 1997) were combined with dispersal behaviour in a simple model (Halley *et al*,1996) The model was constrained to one dimensional dispersal in a linear landscape comprising five different habitat types Although simple, the model has provided a number of insights into the importance of interactions between dispersal and the level of hazards in landscapes, for population persistence It has shown that in a given landscape with a certain spatial and temporal distribution of hazards and, resources, a particular dispersal strategy leads to a particular population size However, too little or too much dispersal results in regional extinction (Halley *et al*,1996) Species with different life history and dispersal strategies therefore tend towards different population sizes in the same landscape (Thomas, 1997) Thus the interaction between life-history strategy, dispersal strategy and landscape structure will affect population persistence and species and genetic diversity at the spatial scale over which the spiders disperse

The current model is configured for a non-specific linyphiid spider, dispersal opportunities (the weather window) are deterministic, and there is no mortality applied to spiders during the act of dispersal The principal goal of the present study is to develop this model by expanding the landscape and dispersal to two dimensions, configuring the population and dispersal dynamics for specific species, increasing the number of habitat types, and incorporating relevant stochastic elements such as weather dependent dispersal opportunities Thus the four essential components of the system listed above will be integrated into a model that will produce output in the form of the probability distribution function of species population size over space and time, enabling persistence or extinction times to be quantified An improved model of dispersal distances has already been developed (Thomas *et al*, *2003* submitted)

Another factor retarding the development of spatially dynamic population models is the difficulty of rigorous testing and validation Linyphiid spiders exist in the collection of 30 years archived suction trap samples from the Rothamsted Insect Survey (RIS) These data, together with our ability to predict dispersal retrospectively from archived meteorological data, and our ability to use our dispersal model and meteorological variables to calculate the catchment area of suction traps, offer a unique opportunity for extensive model validation and hypothesis testing The model can therefore be tested and validated against contemporary field data and RIS data from different landscapes The archived RIS data can also be analysed for historical changes in abundance and diversity of spiders exposed to increasing insecticide usage over recent decades Configuring the model to simulate the increased mortality risks associated with agricultural intensification will provide output to correlate with these observations An important component of the project is to predict and test adaptations to high risks during dispersal in island populations that have been exposed to such hazards on an evolutionary time-scale Finally, we will use the model to assess the effects of landscape structure, patterns of land-use and patterns of agrochemical use, in terms of the potential risk to population persistence and diversity

Material and methods

Field sampling, population dynamics and aspects of dispersal

We are currently studying the following eight farmland linyphiid spider species in detail: *Erigone atra, E dentipalpis, Lepthyphantes tenuis, Bathyphantes gracilis, Oedothorax fuscus, Savignia frontata, Milleriana inerrans, Meioneta rurestris* Field populations are sampled by D-vac suction sampler in eight arable and pasture fields Potential food items (aphids, collembola, and small diptera) will also be quantified Samples are taken throughout the year, with most intensive sampling during the main reproductive periods in summer and autumn The effects of crop management will be quantified by taking samples immediately before and after

field operations. We aim to sample some fields for five years covering 10 generations and at least one complete crop rotation. This will provide model inputs, in particular the mortality due to field operations such as insecticides, harvesting and cultivation. Aerial samples of dispersing spiders are collected with hand aspirator, water traps (Thomas & Jepson, 1997; 1999) and novel bottle traps (Woolley & Thomas, in prep.) to provide field data on species specific differences in the timing, frequency and intensity of dispersal.

Spiders are also kept in vivaria with different levels of food supply. For each of the eight species, life span, egg production and development time are being quantified using methods similar to those of de Keer & Maelfait (1988). Spiders will also be exposed to controlled air currents in simple wind-chambers to elicit ballooning responses (Legel & van Wingerden,1980, Weyman *et al.*, 1995). This will provide further data on species specific differences in dispersal strategy. For each species, dispersal behaviour will be quantified in terms of their probability of dispersing when conditions are suitable, the number of flights attempted before giving up, the duration of ballooning behaviour, the effects of recent feeding history, and differences between probability of dispersal by different age classes.

RIS trap data will provide information on differences in spider abundance and diversity as a function of space by sampling from contrasting landscapes; and as a function of time - over the past 30 years during the period of increased agricultural intensification.

Data of wind speed and direction in daylight hours, when wind speed is below the ballooning threshold of $3ms^{-1}$, will be obtained from the UK Met Office. These data will be used to determine the distribution of the number of hours of available ballooning time per day; the distribution of the number of days per year when ballooning is possible; and the wind speed and direction during each potential ballooning event.

Populations of *E. atra* and *E. dentipalpis* will also be sampled from a number of island and mainland sites.

Use of molecular techniques

Molecular genetic data using a set of "universal primers" for the mtDNA COI and COII genes have been generated to identify immature stages of the spider species from the field samples for demographic components of the model.

The comparisons between the genetic structure of island and mainland populations sampled at comparable distances will use microsatellite markers. This will enable us to test (a) whether the sea is a significant barrier to gene flow (b) whether the isolation is effective enough for island populations to have adapted dispersal behaviour more suited to the hazards of dispersing on an island (c) whether differences in diversity can be ascribed to the physical barrier or differences in dispersal hazard and effective population size. To test these hypotheses we are focusing on *E. atra* and *E. dentipalpis* for which we have already developed enriched microsatellite libraries. It is common practice to infer estimates of recurrent dispersal based on measures of population genetic structure. While meaningful in their own context (i.e. for a specified population genetic model) the usefulness of such estimates as measures of dispersal comparable to those based on field studies/census counts is dependent on how realistic the assumptions of the genetic model are. The major objectives of the microsatellite screening are the three listed above but it will also be possible to derive indirect estimates of dispersal which can provide indicators comparable to those from the modelling and field based measurements.

Model development and simulation

To model dispersive populations in fragmented landscapes we need to integrate novel dispersal models with both existing and novel demographic models. A proportion of spiders, from populations with density defined in space and time, disperse by ballooning at each point by a wind-driven process, moving the spiders a certain distance according to a probability density function. A proportion are lost by exposure to hazards during dispersal so the spider density at any point after a dispersal episode will be the convolution of the number dispersing from each point, and the proportion surviving each dispersal distance. This point density will be augmented by the number of spiders immigrating into the landscape from outside sources, whilst loss of spiders from the landscape will be modelled automatically as part of the dispersal process.

In addition to this dispersal process, the population at each point will be subject to a spatially varying birth/death process, with model parameters also varying over time with the habitat or field. Thus, in an inhospitable habitat a significant proportion of the population will die in each time step; in a favourable habitat the population will increase according to species specific life-history pattern. The full cycle will be modelled, i.e. eggs will be laid, hatch into juveniles, and develop into adults to give the number of adults at the start of the next time step.

Thus, the model describing the entire dynamic of these species is comprised of many simple components which can be pieced together to form a comprehensive description of the underlying stochastic processes

driving the population The component-based nature of the model lends itself readily to specification in graphical form (Lauritzen, 1996) so that the likelihood associated with observed data can be split into a product of simpler conditional distributions greatly simplifying both specification and computation

Graphical or independence modelling, combined with substantial recent advances in computing technology, has effectively revolutionised the way in which we can think about computer modelling of stochastic systems The conditional independence structure of such models allows us to build models in "blocks" which can be added at different times so that the model "evolves" in complexity Therefore, we would start with a basic model and extend it as additional modelling information arrives

Models are represented graphically by a set of nodes and edges, which represent model parameters and their relationships Dependence between two parameters is expressed by the presence of an edge between the corresponding nodes and the full graph provides an explicit map of the model in terms of the inter-dependence between model parameters The model can thus be developed component by component, so that we can start with a very simple model, adding extra levels of complexity in stages The proposed approach is ideally suited to the problem at hand since experimentally, the model will be built component-wise, with dispersal, population dynamics, and the spatial and temporal dynamics of habitats forming separate components which can be independently developed and tested

Once a particular model has been specified there are two separate forms of simulation required The first is for prediction, which can be performed via what is known as "forward" simulation where, having specified the model parameters, we simulate "data" to see the effect of different factors in the model on the resulting population dynamics Essentially, we simulate "data" from the distribution of the data conditional on the parameter values (i e , the likelihood described above) The second form of simulation required is for parameter estimation which is performed via "backward" simulation where we simulate from the distribution of the parameters conditional on the observed data This distribution is obtained via Bayes theorem specifying the "posterior" distribution of the parameters conditional upon the observed data as being proportional to the likelihood and a "prior" distribution specified for the parameters before any data is observed This distribution is typically high dimensional and complex and can only be performed via Markov chain Monte Carlo simulation (Brooks, 1998) The method proceeds by constructing a Markov chain with stationary distribution equal to the distribution of interest Such a chain can be easily simulated using a series of simple updating mechanisms and the distributions of interest may be obtained via empirical estimates from the samples thus obtained

There will also be a strong focus on model validation, both in the empirical sense in which predicted behaviour is matched to that observed and also in terms of formal statistical model determination For example, there is potential for the inclusion of a large number of covariates within these models, thus, in addition to the traditional MCMC simulation techniques, novel reversible jump MCMC (Green, 1995) methodology will be required in order to discriminate between competing models (e g the inclusion or otherwise of different covariates) This will involve the introduction of new move types within the backward simulation algorithm, to allow us to move between models of different dimensionality Empirical estimates of the posterior model probabilities may then be obtained by observing the frequency with which different models are observed within the simulation run

Acknowledgements

This work is funded by the BBSRC under Grant Nos D14032, D14036, D14034 and D14038

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